The Evolution of Pelage Colouration in Primates

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Abstract

Diurnal primates are often vividly coloured. Most commonly, the males are brighter than the females. Some infants have a natal pelage that is bright or, in dichromatic species, similar to the least conspicuous sex. This study examines intra- and interspecific variation in pelage colouration to determine how and why pelage colour signalling has evolved in primates.

Hypotheses concerning the evolution of sexual dichromatism, natal colouration and pelage brightness were tested. The first approach uses three comparative methods, correlating pelage colourations with ecological and behavioural variables. Two methods control for the inheritance of shared characteristics between closely related species. The second approach involves fieldwork to measure parasite load and pelage brightness in two lemur species, one of which is dichromatic. Inter- and intraspecific comparisons were made to test hypotheses proposed by Hamilton and Zuk (1982).

Several forms of natal colouration were identified; one is correlated with the evolution of sexual dichromatism. Species practising polygamy and those displaying natal colouration are significantly brighter. Both sexes in male dominant species have bright rumps.

There is limited support for the Hamilton-Zuk hypothesis; females in *Eulemur fulvus rufus*, a species with female dominance and brightly coloured females show a significant negative correlation between pelage brightness and incidence of the parasite *Lemuricola*.

The mechanism of "bright pelage selection" is proposed for the evolution of pelage communication, where a high status and good health are signalled by the brightest pelage (or rump), influencing mate choice. The brightest sex is dominant, which evolved as a means of discrimination by mate choice for the healthiest, highest ranked individuals. Sexual dichromatism has evolved via persistent mate choice for good health and high rank.

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I declare that the material contained in this thesis has not previously been submitted for a degree in this, or any other University and that it is my own work.

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Chapter One

Introduction

1.1 Outline and Aims

The vividly coloured face of the mandrill, the silver back of the gorilla and the heavy cape of the gelada baboon are examples of secondary sexual characteristics displayed by male primates. Some primates use colour definition to an extreme. For example in *Eulemur macaco*, the black lemur, the male has a sleek black pelage and the female is rusty coloured with ear tufts. Pelage colour differences between the sexes are termed sexual dichromatism. In primates, the male is commonly brighter, but there are exceptions (e.g., *Eulemur fulvus rufus*). Individuals also display variations in hair and skin colour in the form of ornamentations such as beards, moustaches, capes and whiskers. Genitalia can also be brightly coloured. The mandrill's genitalia mimic its vivid facial colours and the vervet monkey, which appears dowdy, has a red penis and blue scrotum. Pelage colour variations are also ontogenetic, signalling the age of an individual. Young individuals can display a natal colouration, which is commonly brightly coloured and very conspicuous, with a quite different appearance to the adult forms. A brightly coloured infant is a curious phenomenon; it would be expected that an infant would be well camouflaged to avoid predation, yet many langurs have vivid orange or white babies. Some primates display both sexual dichromatism and natal colouration, with individuals varying in pelage colour, dependent on age and sex. When this is the case, the infant or juvenile often resembles the mother in colouration until maturity.

The aim of this study was to examine how intraspecific differences in pelage colouration manifested in the forms of sexual dichromatism, ornamentation and natal colouration have evolved in primates. Suggested mechanisms of sexual dichromatism and natal colouration are discussed in this chapter, and previous experimental work discussed.

Two approaches are used to test hypotheses concerning the phenomena of sexual dichromatism and natal colouration. Both approaches use the comparative method.

1.11 Interspecific correlates with pelage colour evolution in Primates

Information on colour variation, ecology and behaviour in primate species was compiled and analysed using comparative methods. Three comparative methods were used to identify correlates associated with sexual dichromatism, ornamentation and natal colouration. Each comparison was organised to test previous hypotheses and identify the evolutionary mechanisms for sexual dichromatism and bright natal pelage.

1.12 Intraspecific colour variation in lemurs

The second part of the study was performed to identify intraspecific mechanisms involved with the evolution of sexual dichromatism. The study is based on the "bright male" proposals made by Hamilton and Zuk (1982), and subsequent experimental evidence. They proposed an association between a brightly coloured pelage and a low susceptibility of the individual to parasitism; bright pelage colour is taken as an index of health, where a brightly coloured individual has reduced susceptibility to parasites. It was hypothesised that sexual dichromatism would be found in species in which parasitism is more prevalent, and that this would be justified by the selection of the most brightly coloured mates. The evolution of sexual dichromatism may be caused by choice (commonly female) for a brightly coloured mate.

Despite the many studies providing experimental and theoretical support for and against the "bright male" hypotheses, no studies have involved mammals. The majority of work has involved birds, with the focus on plumage brightness and female choice for the brightest and most ornamented males (e.g., Read, 1987; Seutin, 1994; Bucholz, 1995). It is not clear why an anthropocentric visual assessment of "brightness" has been used for birds which have a different visual system, as it may have no bearing on the brightness of the plumage visualised by birds. Mammals have a different visual system, and the primates are the most visual of all. This feature is demonstrated by the array of colours used in primate pelages. This study used fieldwork with two species of lemur, one species of which is sexually dichromatic, to collect parasite load and pelage colouration measurements. The two forms of data were compared to identify associations between a bright pelage colouration and a high parasite load in individuals from two sympatric free-ranging captive species.

1.13 Resumé of comparative methods

i) The first method analysed two-way tables for associations between dichotomous variables. There was no adjustment for the evolution of similar characteristics between closely related species. Previous research has often utilised this sort of approach when discussing colouration. The inclusion of this method in the study illustrates the importance of accounting for the evolutionary bias when comparing related species.

ii) The second method of comparative analysis used the computer program

Comparative Analysis by Independent Contrasts (CAIC) written by Purvis and Rambaut (1995). The program allows comparisons to be made between continuous and categorical data for certain traits in a species without a bias towards traits that have evolved between closely related species. A series of hypotheses were tested using CAIC involving pelage colouration and the outputs were analysed statistically. This relatively new program has been used in other comparative studies and was the most appropriate method to use compared with the alternatives which are the Felsenstein method (Felsenstein, 1985), and the older program, MacClade (Maddison and Maddison, 1992).

iii) The third method of analysing the comparative data used a binary method of analysis designed by Read and Nee (1995). This method also accounts for evolutionary relationships between closely related taxa but, unlike the second method using CAIC, it allows two categorical traits to be compared such as the presence/absence of sexual dichromatism and natal colouration.

iv) CAIC was used (as for ii) and the intraspecific variations in pelage brightness and parasite load were compared for two sympatric free-ranging lemurs, using standard statistical methods (see methods).

1.2 Background

1.21 The Social Organisation and Ecology of Primates

The order Primates is composed of around 200 species, divided into two sub-orders: Strepsirhini and Haplorhini. Strepsirhines are commonly nocturnal with a protruding moist nose called a rhinarium, the digits have nails, and a toilet claw, which is used for grooming, forms on the second pedal digit. Specialised scent glands are present and are used in territorial marking and communication. Strepsirhines have 36 teeth, with the lower incisors and canines forming a tooth comb that is also used in grooming (Napier and Napier, 1985). The haplorhines are divided into two infra-orders: Tarsoidea and Anthropoidea the latter of which is divided into Platyrrhini and Catarrhini, which vary in tooth number with 32 teeth in the catarrhines and up to 36 in the platyrrhines. Neither group has tooth combs. Haplorhines have a flatter, shorter face, with a dry nose, eyes that are more forward facing than in the strepsirhines and are adapted for diurnal colour vision. They also have nails, but there is an absence of the toilet claw. Scent glands are most commonly found in the platyrrhines, but occur less frequently than in strepsirhine species. Primates are generally tropical and vary widely in their distribution and habitat. Primates also vary dramatically in morphology and colouration with some vividly coloured species, and others displaying cryptic pelages. Some primate species vary intra-specifically for pelage colouration with young infants or juveniles displaying a different pelage colouration, termed natal colouration. Pelage colour variation between the sexes occurs in strepsirhines and haplorhines, and is termed sexual dichromatism. Sub-species can also differ in colouration due to geographical distribution but this form of colour variation is not considered in this study.

The first attempts to comparatively analyse features in primates were characterised through social behaviour alone. Crook and Gartlan (1966) were the first to examine primates by developing a comparative method. Primates were grouped into five adaptive grades determined by habitat, diet, activity, group size, reproductive unit and presence of sexual dimorphism. Nocturnal, small, solitary primates were classed as Grade I, and the diurnal, large, harem grouped savannah species such as baboons, were classed as Grade V. Two problems are caused by categorising into discrete groups; continuous variables, such as group size are arbitrarily graded, and breeding system and group size do not always correlate, limiting the grade into which a species can fit (Krebs and Davies, 1993). The procedure of categorising primates based only on social behaviour was described as "allocating gross ecological categories to species making little attempt to examine differences within, as well as between the ecological groups" (Clutton-Brock and Harvey, 1977 p.1). It has consistently been shown that attributing a social behaviour to members of the same ecological category is inaccurate due to the number of variables involved (Altmann, 1974; Clutton-Brock and Harvey, 1977; Harvey and Pagel, 1991; Bronkiowski and Altmann, 1996). Therefore, to classify and attribute specific variables to a species is difficult. The number and description of the variables depend upon the purpose of the comparative analysis, which should be tailored to answer specific questions. There are two main problems associated with making a comparative analysis between species' ecological and social characteristics (Clutton-Brock and Harvey, 1977). The first problem is that if only data obtained from ecological studies is used in the comparison, sample size will be small and biased by the availability of study groups. Problems will also arise from varying the methods of studying and assessing the variables, which could contribute to making incorrect associations of characters between species. The second problem is not in the categorisation of the variable, but the

quantification. This is the case when several sources are used and an average value must be found from the various sources, possibly biasing the result of the associations through using the median. The number of categories used in a comparison can be daunting. The use of many categories will best describe the features of a species, but using characteristics specific to a small group (or to one species) will make the characters useless for comparative purposes and therefore redundant. Alternatively, too few characters in a comparison may be insufficient to determine the required variation between the species. For example, members of the order Primates share certain characteristics. If only these characteristics are used in a comparative analysis of primate species there would appear to be little or no evolutionary variation. There must be careful selection of the number of characters and their nature for the purpose of the comparative analysis.

The ecology and social structure of primates were considered together in a comparative analysis by Clutton-Brock and Harvey (1977). They grouped three different features of primate ecology into combination categories: lifestyle, nocturnal or diurnal; habitat location, terrestrial or arboreal; and diet folivory, insectivory, or frugivory. In total, there were seven combinations of the features that were exhibited by living primate species, and each category was used for each species in the comparative analysis, instead of the combinations of three separate lifestyle characteristics. Other comparative analyses have considered lifestyle attributes separately (Harvey *et al.*, 1987; Barton, 1996), and the nature of grouping or separating the characteristics must also be considered for each comparative analysis.

Social organisation within the order Primates is complex and can vary between related

species. There are also examples of convergence of social organisation between distantly related species due to similarities in ecological adaptations; for example, chimpanzees and spider monkeys practice similar social behaviour (Wrangham, 1987). The ecological pressures exerted on a species define the behaviour in terms of social system. The evolution of the social organisation of a species may be constrained by traits that are shared between closely related species (Wilson, 1975). These traits, such as body size, presence of sexual dimorphism, nocturnality, etc., will put constraints on the social interactions possible. For example, in strongly sexually dimorphic species where the male is much larger than the female, male dominance is already asserted due to size difference. In species with similar sized sexes, male dominance could be less pronounced or in favour of the female as in *Lemur catta*, the ring-tailed lemur (Napier and Napier, 1967).

The components of social organisation are group size, mating system, home range, body size, and dominance. They are all related to a species' environment and may not be fixed since, for example, solitary foraging species will tolerate each other at the site of food abundance (i.e., one particular fruit in season). The group size of a species is the average number of individuals living together for each species. This will be dependent on the mating system, and hierarchy practised for each species. Richard (1985) described the social organisation of primates as being dependent on a group of attributes: the degree of tolerance of individuals, territorial defence, how sexes interact with each other and within the sex.

1.22 Habitat

Primates mainly inhabit the tropical regions of the world between the tropics of Cancer and Capricorn (Smuts *et al.*, 1987); there are over 200 recognised species distributed across 92 countries. There are four main regions which primates inhabit: the Americas, South and temperate Asia, Africa, and Madagascar (Wolfe and Sleeper, 1997). The distribution of monkeys is often referred to as Old World and New World. Old World refers to species distributed throughout Asia and Africa, including baboons, colobines, langurs, guenons and macaques. New World monkeys are found in Mexico, Central America and South America, and include capuchins, howlers, titis, spider and woolly monkeys. Strepsirhines are distributed throughout the Old World; lemurs are only found in Madagascar, bushbabies and pottos are from Africa, and the lorises are found in Asia. The great apes and lesser apes comprise the Hominoidea; gorillas and chimps are found in Africa, the gibbons and orangutans are distributed throughout South Asia, and genus *Homo* has a Worldwide distribution.

Primates, although generally tropical are found in three of the four groups of biomes found in the world; the exception is the sub-arctic and arctic biome, which are uninhabitable to primates (Richard, 1985). Most primate groups are distributed throughout the tropical biomes, and the most common areas for primates to inhabit are the rainforest, seasonal forest and woodland habitats. Members of the Cercopithecidae inhabit the largest range of habitats; they are found in temperate forest, grassland and scrub and even in the sub-alpine and alpine areas. The northern macaques and langurs inhabit the mountainous areas of Japan and the Himalayas (Napier and Napier, 1967).

The nature of the habitat in which a primate lives influences the lifestyle of the species. Lifestyle is usually described by a set of ecological and behavioural features that are suitable for the environment a species inhabits. Primates are often described as arboreal or terrestrial, classified by the length of time a species spends in the trees or on the ground. This will be largely dependent on the habitat, substrate, and the nature in which a primate feeds (Napier and Napier, 1985). The mode of feeding is described as foraging or banqueting. A species which is described as a forager depends on dispersed patches of food resources such as insects or fruit, and a banqueter has a large and constant food source, such as leaves (Oates, 1987). Many primates feed on an insectivorous or frugivorous diet, supplemented by foliage; most primates are a combination of the two types. The majority of primates are arboreal and folivorous and/or frugivorous. Terrestrial species often have patchy food sources and travel on the ground to feed; for example, geladas and baboons feed on young shoots, seeds and leaves and often supplement this diet with fruit and other animals (Napier and Napier, 1985). The habitat also has some bearing on a species displaying terrestriality; savannah baboons spend a lot of time ranging the grass and scrub-lands of Africa where there are fewer trees available (Altmann, 1980). A species in an exposed habitat is more susceptible to predation (Hrdy, 1970), and may therefore display a more cryptic or dull pelage than arboreal species. Many other factors will also influence the terrestriality or arboreality of a species: predation, seasonal food availability, body size, weather and competition for food resources (Oates, 1987; Bronkiowski and Altmann, 1996).

1.23 Categorising the activity pattern of a species

Primates display a range of day and night forms of activity with morphological adaptations to suit the lifestyle. As all assessments of brightness were made visually or measured with a spectrophotometer, to assess the brightness of a species or individual's pelage colouration, it is important to consider how a species perceives brightness and colouration. There are three basic lifestyles displayed by primates with reference to activity: diurnal, nocturnal, and cathemeral. Some lemurs are described as cathemeral as they are most active at dusk and just before dawn (Tattersall, 1982). It has been demonstrated that lemurs, tarsiers and the night monkey do possess cones in their retina, although only one type of cone pigment, allowing only dichromatic colour vision (Jacobs, 1981).

Nocturnality is thought of as a primitive condition for activity pattern in mammals. When considering primates, it would be easy to consider nocturnal primates as possessing the ancestral form of vision. However, the pure rod retina that characterises the vision of most nocturnal species is not found in all nocturnal primates. *Aotus*, the owl monkey, is the only anthropoid to display nocturnality, yet have a duplex retina of rods and some cones (Jacobs, 1981). The duplex retina is a characteristic of diurnality and is found in all diurnal primates. Hershkovitz (1977) suggests that the primate lifestyle division of diurnality and nocturnality evolved after the ancestral placental species that were crepuscular. They would have possessed an ancestral duplex retina, from which, the rod retina of nocturnal primates has developed and the duplex retinal system of diurnal and crepuscular animals. This would mean that the nocturnal retinal structure is not the primitive form as imagined, but specialised in nocturnal strepsirhines for nocturnal vision.

Both Napier and Napier (1985) and Bearder (1987) however, consider the ancestral primate to have been nocturnal, with the subsequent evolution of nocturnal strepsirhines and diurnal ancestral anthropoids (of which the true lemurs, indri and sifaka are the exception for strepsirhines, and the owl monkey the exception for the anthropoids). The true lemurs are commonly diurnal or crepuscular and the indri and sifaka are diurnal.

Primate nocturnality is also associated with the possession of a tapetum lucidum that reflects light back into the retina to effectively double the amount of light entering the eye. This is absent in the owl monkey and the tarsier (Hershkovitz, 1977; Napier and Napier, 1985; Bearder, 1987). A nocturnal species can be described as being small with a high energy diet, poor manipulative abilities, solitary foraging, and with a reliance on olfactory and auditory communication (Bearder, 1987). Bearder further describes diurnal primates as being larger with a more varied diet including folivory, improved manipulative abilities, gregarious foraging habits, and a reliance on visual acuity and colour vision, accompanied by larger brains to body size. This applies to the majority of diurnal or nocturnal species with a few exceptions.

1.24 Group size and mating system

Variables that are used with reference to mating system and grouping are: average number of adults in a group, polygamy/monogamy, and multi/single male grouping. The mating strategy is commonly associated with the group size and structure. There are three common forms of mating structure. Polygamy, having more than one mate at the same time, which can exist as polyandry (female consorting with several males) or

polygyny (male consorting with more than one female) (Henderson, 1949). Monogamy is commonly practised in species living in family groups with one adult male and female pair and their offspring. It is not restricted to one group of primates it is displayed in all primate groups with the exception of the great apes. However, there are very few monogamous species within these taxa: *Hylobates, Indri, Tarsius spectrum, Callicebus, Aotus, Simias, Cercopithecus neglectus* and *Presbytis potenziani* (Napier & Napier, 1985; Bearder, 1987).

There are three main types of grouping in primates (Napier and Napier, 1985):

1. Multi-male: more than one adult male with several females and offspring
2. Single-male: one adult male with several adult females and offspring
3. Family groups: one adult pair and their offspring

Some species do not fit into one specific category; for example, chimps form large multi-male groups that are made up of sub-groups. Nocturnal species have one-male groups of one male to several separate females with each female being visited by the resident male; these include Galago, Loris and Lepilemur (Napier and Napier, 1985). Gelada and hamadryas baboons herd together at night into communities of up to 100 individuals (Altmann, 1980), but both have single male mating structures.

Single male systems are represented in all infra-orders: strepsirhines and haplorhines (tarsiers, New and Old World monkeys, and apes). The single male must be the dominant figure of the group, rejecting other males, including juvenile male offspring as they reach maturity. The juveniles are forced to migrate from their natal group to form new groups or compete for an established group by displacing the dominant male. The hanuman

langur, *Presbytis entellus,* often forms large bands of sub-ordinate males who may never compete for a group of females (Napier and Napier, 1985). Males gain control over a female group using aggression and by fighting the male leader to expel him from the group (Dunbar, 1988). Males who lead single-male groups or harems, must be large and strong to fend off other competitors for the group (Dunbar, 1988). The female must also be willing to accept a new male, as the leadership is not a certainty once the leader is expelled from the group; it may take many months for the group to accept the new leader. In many species the subordinate males live on the periphery of a group within the home range to take advantage of chance matings out of sight of the dominant male (Bateson, 1983). Polygamy is common in single-male groups in the form of polygyny. Males must be large to compete successfully with other males and therefore, there is often extreme sexual size dimorphism. The intensity of sexual selection increases with the reduction in the number of one sex, i.e. in one male groups (Emlen and Oring, 1977). Secondary sexual characteristics should be more apparent in single male groups. Sexual selection for secondary sexual characteristics is also associated with polygamy with the increased potential for multiple mate monopolisation, the greater the potential for sexual selection and polygamy (Emlen and Oring, 1977).

Examples of the monogamous family group are also seen across the order Primates. They exist as a nuclear family unit of a mated male and female and their offspring. At the onset of sexual maturity, juveniles are subjected to aggression from both parents to "encourage" them to leave and find a mate (Napier and Napier, 1985). There is less male-male competition for a mate as most practice monogamy; there is therefore, little or no sexual dimorphism. In general, monogamy is not the best way of maximising a male's reproduction. There must therefore, be benefits outweighing the costs of foregone

mating opportunities in practising monogamy in primates. Clutton-Brock and Harvey (1977) outlined two potential benefits: a) more offspring survive when the female is assisted in parenting, and b) because females mate selectively with monogamous males. In the case of the primates, this care will be in the form of protection, infant carrying and territory defence (Clutton-Brock and Harvey, 1977). Parental care is especially necessary when species commonly produce twins in the Callitrichidae (Clutton-Brock and Harvey, 1977). Limits on territory size may select for the practice of monogamy because males may be unable to defend access to more than one female (Crook, 1972). It is predicted that species that live in family groups have a low population density, practice territoriality and often produce twins (Clutton-Brock and Harvey, 1977).

Multi-male groups tend to be found where female group size is larger (Altmann, 1974). Male dominance hierarchies determine access to females (Cowlishaw and Dunbar, 1991). Males must compete within the group using aggression to exert their dominance over other males. The females remain in their natal group and males disperse (Napier and Napier, 1985). Subordinate males are often solitary or living on the periphery of the group until accepted. Multi-male grouped species are polygamous. Two preconditions for the evolution of polygamy are outlined by Emlen and Oring (1977): multiple mates must be defensible by individuals, and the animals must possess the ability to utilise the environmental potential. Therefore, in a polygamous system, one individual must monopolise others with respect to mating and be able to defend the territory in which the harem/group live.

The number of males in a group depends on several factors, including the richness of habitat (multiple males may be more tolerated in a source of resource abundance), and

the tolerance of the alpha males for subordinants (Richard, 1985). The number of males is dependent upon the costs and benefits for a species at a given time (Clutton-Brock and Harvey, 1977). The costs of tolerating other males in the group are a reduction in breeding success, increased male-male competition, and energy expenditure in competing for resources. The benefits could be in territory defence against other males and for an increased fitness due to kin selection, if the male is related. Crook (1972) suggested that savannah species are less prone to a lack of food resources, due to the nature of the habitat, so competition pressures between males is reduced allowing the formation of multi-male groups. Clutton-Brock and Harvey (1977) however, pointed out that multi-male troops are present in several rainforest species, such as colobus monkeys and howlers. Crook (1972) also suggested that multi-male species are a response to predation pressure, yet large species such as baboons and howlers have fewer predators than smaller arboreal monkeys. Ridley (1986) considered the duration of the breeding system to be associated with the number of males in a group, and the mating system. In species with a very short period of receptivity, as in *Lemur catta,* a single male will be unable to breed with every female in the group as females are only receptive for 1-2 weeks during March and April (Tattersall, 1982). The reproduction of the group would be more successful if other males were to also mate with females during the short period of receptivity. If females become receptive at different times, then polygyny could be practised by a single male (Trivers, 1972). Thirty-three primate species were analysed for the duration of the breeding season and compared with the number of males in a group using the Felsenstein comparative method (Ridley, 1986). There was a significant correlation with single male groups when breeding season was long and multi-male groups when the breeding season was short. There are thus four reasons for living in multi-male groups: protection against predation, defending resources, increased foraging

efficiency and territory size, and increased available care for infants (Dunbar, 1988).

1.25 Dominance

Dominance is defined as the superiority of an individual over others, which refers to first access to mate, resources, territory, etc. Dominant status occurs in both sexes and in some primates it can be inherited; for example, in macaques, baboons, and vervets, the dominance of offspring is dependent on the dominance rank of the mother (Harcourt and Stewart, 1987). In this particular study, the authors also correlated dominance rank with the body size and age of an individual, but found that kinship was the most significant factor in determining the rank of an individual. A study by Cowlishaw and Dunbar (1991) related the dominance rank of males with the mating success of individuals from the same age group. Seventy-five study groups were examined across a range of primates to provide support for the "priority of access models" proposed by Altmann (1962). This theory has had further support from single species studies. It has been demonstrated that in the mandrill, *Mandrillus sphinx,* which displays single male grouping into harems, the dominant male sires 80-100% of the offspring (Dixson *et al.*, 1993). In multi-male systems, Pope (1990) showed that the majority of infants were sired by the dominant male in red howler monkeys, *Alouatta belzebuth.* The same was true for single male groups that are also commonly formed in this species. Therefore, the dominance of an individual has some association with mating success. If it is favourable to be dominant, then what limits the evolution of more aggression and competitive characteristics? Packer *et al.* (1995) conducted a study on 138 female baboons to identify any costs of being a highly ranked dominant individual. It has been suggested

that the most dominant individuals should also be the "fittest", with reference to reproduction potential. Higher ranked females were not found to be the "fittest" in the group due to a higher frequency of miscarriages; it was suggested this was due to stress related reproductive failure. A counter-selective force acts to cause the females to be aggressive to attain the highest rank, but the individual becomes stressed in the dominant position due to competition from other members of the group, which causes infertility. Three mechanisms for the high infertility of dominant females were suggested. Low ranked females create social coalitions with males, allowing the impact of the short-term costs of being subordinate to be minimised. High ranked females were often chronically infertile, which could be due to the impact of disease caused by stress affecting fertility. There may be two types of females that attain a high ranked position; and one may have the endocrinology to deal with stress better than others. The impact of the stresses on dominant individuals may be dependent on the group size, and thus the stresses caused through competition for rank. Very few primates are female dominant, which is probably related to the extensive presence of sexual size dimorphism throughout the order. The true lemurs, genus *Eulemur*, display very little dimorphism, and the females are dominant (Tattersall, 1982). This suggests a relationship between size dimorphism and dominance. *Ateles fusciceps*, the spider monkey, shows some reversal of size dimorphism where the female is slightly larger (<5% difference) and females are dominant.

1.26 Body weight and sexual size dimorphism

Primates can vary enormously in their body weight with male gorillas weighing 160 kg, 2000 times the weight of the *Microcebus murinus*, the dwarf lemur, that weighs in at

0.08 kg (Harvey *et al.*, 1987). Such large differences in body size are likely to have profound effects on variation in other traits (Martin and Harvey, 1985). There are several problems associated with comparing body weights amongst species. The first, is in obtaining accurate measurements of individuals representative of a species adult size, as wild animal measurements are limited by the availability of study groups. Measurements of body weights from captive animals will also differ from wild animals due to the improved diet and the constant availability of food. A second problem is that measurements are not made at various stages throughout an individual's adult life, to gain an average body weight with reference to age for a species (Richard, 1985). Another problem in using body weight measurements from the literature is they are often given as an "average" body weight of the two sexes. The phenomenon of sexual size dimorphism, where there is a variation (sometimes very large) between the sexes is not accounted for. When obtaining body weights from the literature for comparative analysis, each must be used wisely to insure against using biased data.

Why are primates so variable in body size? Males are considered to be larger than females to avoid competition by exploiting different food sources (Selander, 1972) or, through intrasexual selection (Darwin, 1871). Western (described in Richard, 1985), compared life history variables (gestation time, age at first reproduction, and life span) with body weight in African carnivores, ungulates and primates. The comparisons demonstrated a relationship between each life history variable, with an increase from small to large sized species. This variation was not uniform, as the rate of increase differed between species. In all three groups, however, the larger the animal was, the later an animal reproduced and the longer the gestation period. Primates had the longest gestation time and took longer to reach reproductive age, but lived longer than species of

similar body weights from the ungulates and carnivores. The longer gestation time and slower growth rate of primates was suggested by Jerison to be related to the larger brain size in relation to body size of primates (Gould, 1975). The type of species must also be considered when making comparisons using body weights. Precocial species, born at an advanced stage of development, cannot be directly compared with altricial species, where there is a high dependency from the newborn due to the slower maturation of the fetus (Harvey *et al.*, 1987). Fortunately, when making comparisons between primates, this consideration is unnecessary.

There are many biological and ecological features related to the body size of a species. Nocturnal species are generally small, while diurnal species can be small or large. Cryptic species also tend to be small (Harvey *et al.*, 1987), and terrestrial species are larger than arboreal species. This is probably linked to the method of locomotion used, with larger, brachiating species, such as the orangutans being large. Species that are quadrupedal branch walkers require a small body size to be supported on small tree branches (Fleagle, 1988). Diet is a major factor in the body size of a species. The metabolism of an individual is related to body weight, where there is an increase in the basal metabolism with an increase in body weight (Kleiber, 1961). Basal metabolism requirements increase with body weight by a factor of 0.75. This means that, in general, the larger a species, the lower the quality of food required compared to smaller species as the energy requirements of the smaller species are less per unit body weight (Harvey *et al.*, 1987). An insectivorous diet is a much higher source of energy than a folivorous diet due to the high levels of animal protein. It was shown using studies on primates that there is only a slight increase in the amount of insects consumed with an increase in body weight, due to the time required foraging for insects. This is a constraint on the larger primates forcing

them to switch from an insectivorous diet to frugivory and folivory (Napier and Napier, 1985).

Body size appears to closely correlate with many life history, biological and ecological variables. Bonner (described in Harvey and Pagel, 1991) demonstrated that, across the range of species present on Earth from bacteria to elephants and trees, there is a relationship between the generation time of a species and body length. Numerous factors can be related to and correlated with body weight from the testes size of primates to maximum population densities.

Sexual size dimorphism is a form of secondary sexual differentiation and has no role in copulation (Darwin, 1871). Sexual size dimorphism is a difference in body size or body weight between the sexes where the male is commonly larger than the female, although in primates there are some exceptions which will be mentioned in the discussion. Sexual dimorphism is manifested in many forms. The main morphological differences between the sexes are: size (including body weight and body dimensions), dentition, cranial features such as a sagittal crest, locomotor apparatus (muscle and skeletal dimensions), internal organs, external features (colouration and ornamentation), and maturational, seasonal or morphological changes associated with reproductive cycles (Leutenegger and Chevreud, 1985).

Females are commonly larger than males in animals; this association obtains because egg production is linked with body size. Therefore, the larger the individual, the more energetically favourable this is for egg production (fecundity) (Darwin, 1871). This case especially applies to smaller species such as insects. In mammals, this size variation is

commonly reversed. Darwin (1871) suggested larger males were selected for by the male-male competition for a mate. Since Darwin's proposals on the subject of sexual size dimorphism, quantitative support has been provided by numerous studies (Andersson, 1994). Two hypotheses were outlined by Rodman and Mitani (1987) with reference to sexual size dimorphism. Sexual selection acts in one of two ways: intersexual, which is caused by mate choice exerting a selection pressure for a particular set of characters, or intrasexual competition between males for mates, which selects for characters that increase an individual's success over other competitors. Either mechanism may be exerting selection pressure on the male sex for larger body size. Sexual size dimorphism could have been selected for ecologically to reduce the intra-specific competition for food resources (Selander, 1972).

The advantages of variations in size between the sexes have been outlined by Andersson (1994).

Larger males: dominance in male contests for females, lengthened endurance, an increase in success during male-male competition, females choosing the largest male

Larger females: increased fecundity; increased ability in parental care; dominance over males for resources

There are also some advantages in being the smaller sex of the species:

Small males: resource dominance when more manoeuvrability is required, early maturation, increased reproduction rate

Small females: resource dominance when more manoeuvrability is required, increased reproduction rate due to a shorter generation time and early

maturation, more affective allocation of energy resources into offspring production.

The list above outlines the fact that selection for a larger sex is not only dependent on the genetics of a species. Ecological and social factors must also be considered to have an influence on a species being size dimorphic. There are considerable sexual size differences in the large apes, such as the gorilla and the orangutan, where the female is only half of the body weight of the male (Harvey *et al.*, 1987). The activity and the habitat of primates only had an indirect effect on the evolution of weight dimorphism (Leutenegger and Chevreud, 1985). 83% of the variation in body weight in primates was attributed to differences in species body weights alone, and less than ten percent of the total effect on size dimorphism was contributed to by mating system and diet, contrary to the suggestions of Selander (Rodman and Mitani, 1987). Clutton-Brock (1985) questioned the common association between the mating system of polygynous primates and the evolution of sexual size dimorphism, as first noted by Darwin. Associations of sexual size dimorphism have also been suggested to correlate with terrestrialism (Clutton-Brock *et al.*, 1977) and genetic variance in body size attributing to directional selection pressures for sexual variation in body size (Leutenegger and Chevreud, 1985). Therefore, the factors that are associated with sexual size dimorphism are as numerous as the factors selecting for any forms of sexual dimorphism, such as pelage coloration variation.

1.27 Ornamentation and sexual dichromatism

Pelage colour variation between species is often a form of species recognition, whereas colour variation within a species could be cause by sexual selection. Colour variation within a species in the form of sexual dichromatism (where males and females are different in colouration) could be caused by choice for a particular type of mate, where individuals are selecting for difference between individuals and not similarities (Andersson, 1994).

The most conspicuous sex differences occur in primate colouration due to their advanced colour vision (Jacobs, 1981). Darwin (1876) described differences between the sexes in monkeys as uncommon, with usual differences in colour between sexes occurring in naked parts of the skin or through the presence of a mane, beard or whiskers. The first common example is swelling and reddening that occurs in females when they are in oestrus, often in large groups with several males. This may be a result of sperm competition caused by the male-male competition for females (Andersson, 1994). Oestral reddening is common in primates and draws attention to the female's reproductive area when ovulating (Chance and Jolly, 1970). The gelada, *Theropithecus gelada,* is known as the "bleeding heart baboon", as females have a hairless throat and chest surrounded by vesicles, which become scarlet during oestrus, signalling they are ready to mate (Schultz, 1969). The colour changes are often cutaneous around the genital area and are due to the visibility of haemoglobin under the skin (Fox and Vevers, 1960). These cyclical and seasonal changes are not considered in this study.

Skin colour variation can also be a feature of the genital regions of males, most

commonly in the Old World monkeys (Cercopithecoidea). Some of the cercopithecoids have a red penis surrounded by a blue scrotum, often the only bright areas of colour on an otherwise dull pelage (e.g., *Cercopithecus aethiops*). The mandrill has a similar genital colouration, mimicked in the face, which is reported to become more vivid when a male becomes exited (Darwin, 1876). The face of the mandrill could be used in contest competition between other males (Wickler, 1967). Bright skin colours are commonly exhibited on the face in the form of spots, stripes and patches of colour. *Cercocebus torquatus* have white eyelids highlighting their faces and expressions that are probably used in male competition (Napier and Napier, 1985). Many cercopithecoids have brightly coloured faces that are highlighted by beards and manes. In all cases where there are brightly coloured skins, these are not present in the infants and are attributable to sexual selection (Darwin 1876). These colourations may, or may not be acquired by both sexes, and are usually only acquired in the males, but are transmitted evenly to the offspring of both sexes. Ornamentations are also commonly formed with hair, often in the forms of beards, manes or whiskers. Male orangutans, *Pongo pygmaeus,* have a large orange beard, or the beard can be more pronounced as in *Pithecia satanus,* or be in the form of a cape as in the males of *Theropithecus gelada* (Napier and Napier, 1967). These hairy areas were considered to be for protection of the neck and chest by Darwin (1876). Hair ornaments can be present in both sexes, but may be of a different colour; for example *Ateles* spp. have ruffs which are yellow in the male and white in the female (Napier and Napier, 1985). Body parts can also differ between the sexes in colour, such as the tail of *Cercopithecus cephus,* the moustached guenon, which is chestnut in males and grey in females. Often crowns and backs have some distinction in colour between the sexes. The silver back of the adult male gorillas distinguishes not only between the sexes, but also from the younger, less dominant males where the silver back is absent (Chance and Jolly,

1970). Increased hair growth in males could be related to threatening behaviour; this hair is commonly frontal in primates, and the presence of hair that is coloured to contrast with the face can increase the appearance of size (Andersson, 1994). Contest competition and female choice could be exerting an influence on male ornamentation (Andersson, 1994). Ornamentation differences were only considered with reference to female ornamentation (see Appendix 1.7). Reasons for the presence of female ornamentation may be due to females choosing less male ornamentation, or could be a result of male choice. This mechanism will be considered further in the discussion.

Cunningham (1900) suggested an alternative to Darwin's theory of sexual selection with reference to skin colours and ornamentations. He proposed that these colours and ornaments were derived from physiological effects on the body over generations, causing the evolution of the condition. The example he gave was the physiological effect of rump scratching in the baboon, *Papio hamadryas*. He noticed this was very common and was often used as a signal to other members. The scratching effect causes an increase in blood flow to the area, hence a red rump. Over generations of scratching, the rump is redder, caused by a permanent increase in blood flow to the skin surface. The scratching behaviour continues, but the behaviour becomes redundant. This mechanism may now seem fantastical and very Lamarkian, but at the time had been seriously considered as a mechanism for the large ruffs and beards around the neck acting as protection from constant biting (Darwin, 1876).

Examples of sexual dimorphism are common throughout the primates, but the presence of a sexually dichromatic pelage is rare. In species that display sexual dichromatism the adult male is commonly eumelanin (black) dominant for pelage colouration with monochromatic hairs, and the female is often dominantly phaeomelanin (red) coloured

with banding on individual hairs, as in *Lemur macaco* and *Pithecia monachus* (Hershkovitz, 1977). The onset of a sexually dichromatic coat occurs only at sexual maturity and therefore must be the result of sexual selection (Darwin, 1876). Ruminants commonly display sexual colour differences, more than in any other order, but the primates display the widest range of colours in any mammal (Hershkovitz, 1977). Species such as the mandrill (*Papio sphinx*) are vividly coloured with reds, blues, yellows, orange, white and gold to highlight the face and genitalia. There are representative species that are truly sexually dichromatic in each infra-order (see Appendix 1.8).

1.28 Natal colouration

In species where natal colouration occurs, the pelage is usually replaced by a juvenile or adult pelage between 2-6 months of age, the period varying between species. Colours can contrast dramatically with the adult pelage; for example, infants of the dusky leaf monkey, *Trachypithecus obscurus,* are bright orange whereas the adults are almost all brown/black in colour with patches surrounding their eyes (Wolfe and Sleeper, 1997). Infants can also display minor differences from the adult pelage, as with infant chimps who are paler skinned and display a small white tuft on their rump until weaning at 4-5 years (Napier and Napier, 1985). Only gross differences between infant and adult pelages are considered to display natal colouration for the purpose of this study (see Appendix 1.8). Natal colouration may be an example of synchronous melanogenesis, where several forms of coat colour in one species have evolved independently and can therefore be at different stages of chromatic evolution (Hershkovitz, 1977). This process of "moulting"

is a discrete change from one chromatic hair colour to another, caused by the regulation of melanin production by the melanocytes, and is associated with a distinct stage of development. This phenomenon of moulting is also seen in seasonal species where coat colour changes from one colour to another, often from summer colour to white in the winter for arctic/sub-arctic species, (e.g., the snowshoe hare).

1.3 The Chemistry of Colour

In 1870, John Tyndall described colour as "the extinction of certain constituents of white light within the body, the remaining constituents which return to the eye imparting to the body its colour" (Fox and Vevers, 1960, p.1). Mammals are generally dull in colour, with the exception of primates, who are the only group of mammals to exhibit blues, greens and reds in their pelage (Fox, 1940). To study the nature of pelage colouration in primates the mechanism of how an animal appears to be a certain colour must be understood. There are several methods for an animal to display colour; these are highlighted by Rowland (1979):

1. The most common, is the use of integumentary pigments for the absorption or reflectance of light.
2. A physiological mechanism concentrating or dispersing pigment at will, using chromatophores to regulate pigment production and dispersal.
3. Reflection of light causing structural colourations with, or without the presence of pigments.
4. Adornment of colours using coloured exudates or ornaments to adorn

bodyparts.

5. Production of visible energy using bioluminescence.

Primates use the first three methods to produce colours with striking effect. There are three types of structural colour, caused by scattering, inference and diffraction of light. Structural colours can act by scattering light, commonly known as Tyndall scattering after John Tyndall. Scattering reflects the particles of short wavelength light creating blues and purples, as in the blue face of the mandrill (Fox and Vevers 1960). This process works by the procession of light hitting minute air spaces in the skin or hair, reflecting blue light that can be further intensified by the presence of melanin (see below). This process is the same method of making the sky appear blue. The colour white is also caused by the scattering of light. In hair, air spaces in the solid translucent keratin cause the white colouration. Inference is caused by the presence of inorganic solutions causing the reflection of light, such as oil on water. This method causes iridescence in animal colours. The reflection of light is more apparent when the background is dark. Animal iridescence uses air spaces divided by evenly spaced thin lamellae, which are coated in melanin (Fox & Vevers, 1960). Diffraction, the method of creating iridescence, is rare in mammals, but common in insects where parallel lines on hard shiny surfaces diffract light and cause an iridescent sheen, as on a beetle's carapace (Vevers, 1982).

Pigments are molecules that are often organic and unsaturated, with the intensity of colour increasing with the number of double bonds present (Fox & Vevers, 1960). Other molecules can have an effect on colour by shifting the wavelength absorption of light. There are many types of pigments: sclerotin caused by the tanning of protein, omochromes, carotenoids, porphyrins and bilins (including haemoglobin), quinones,

which are common plant pigments, guanine, and flavins (Fox & Vevers, 1960). Melanins, haemoglobin and carotenoids are the commonest pigments in animal pelage.

Melanin is the black/brown pigment found in animals and has many different forms. The main two in animals are eumelanin producing black colours, and phaeomelanin producing reddish colours. Their precise structures are unknown due to their insolubility in solvents (Vevers, 1982). Melanin is present in a granular form, and is less than 1μm in diameter and is often attached to proteins. Melanin is found in the melanocytes of fur and skin, where it is produced. The activity of melanocytes determines the intensity of the colour, ranging from yellow to brown to black. In animals, melanin is the most dominant pigment and produces colours either alone, or in conjunction with structural effects to scatter light and create different colours. Hormones, seasons, low temperatures, active movement, light, other chemicals (such as lecithin) and genetic factors (albinism), all affect the activity of the melanocytes, causing a darker or paler colour (Fox and Vevers, 1960) The main function of melanin in animals is to protect the underlying tissues from visible and ultraviolet radiation. It may also function as a strengthener in hair, chaetae, claws and other organs (Vevers, 1982), but its use in colour as a form of communication, or to make an animal cryptic is also vital.

Carotenoids are an abundant pigment of plants and animals, causing the familiar yellow, orange and red colours. In animals, they are commonly dissolved in fats, and were previously known as lipochromes for this reason. Although carotenoids are found abundantly throughout the animal kingdom (e.g., the yellow colour of body fat and the creamy colour of milks), animals cannot synthesise carotenoids. They must be obtained

through the diet directly or indirectly from plants. However, the structure of carotenoids can be altered in animals from one form to another. For example, the most abundant type of carotenoid in animals is astaxanthin, but this is rare in plants, found only in a few types of algae. This form of carotenoid therefore must be processed after ingestion by animals (Fox and Vevers, 1960). The implications of obtaining carotenoids from the diet are discussed below.

Haemoglobin is a derivative of porphyrin, composed of a protein attached to a circular haem ring (Vevers, 1982). It is haemoglobin in the red blood cells that cause their characteristic colour. This red colouration can be seen through the skin and can therefore be used as a method of colouring the skin. Skin colour is regulated by the capillaries that increase or reduce the blood flow to the skin surface. This can cause either the red colouration seen in the rumps of baboons, or the dark red colour in pregnant baboons, and the temporary colouration of seasonal oestral reddening often seen in mature female primates.

Hair colour is the main contributor to the colouration of primates. Hair colours are more limited than skin colours, as the main contributor to hair colour are pigments. The patterning and nature of the pelage colour of an animal depend on the position and function of individual melanocytes (Fox and Vevers, 1960). Hair bulbs contain melanocytes with the colour of each individual hair being dependent on the metabolism of the melanocytes. Each hair can be monochromatic or banded with different colours, often dichromatic. Banding of single hairs is termed agouti and is the most primitive and common pattern of pelage hairs in animals (Hershkovitz, 1977). The most common patterning of single hairs in the agouti form is the serial banding of phaeomelanin and

eumelanin. *Saguinus fuscicollis,* the saddleback tamarin, displays a characteristic 3-2 banding pattern, where there are three bands of phaeomelanin and two of eumelanin along the hair. This pattern appears to be the most common patterning of animal hairs (Jacobs *et al.*, 1995). Not all hairs are banded; some primates such as *Leontopithecus rosalia*, the golden lion tamarin, have monochromatic hairs coloured solely by the saturation of phaeomelanin (Hershkovitz, 1977). The principle of metachromism was first suggested by Hershkovitz (1968). He proposed that hair originates in the agouti form and becomes saturated with eumelanin or phaeomelanin by one of two pathways, which is progressively bleached to the white form, as seen in albinos.

The process of saturation leads to a red colouration for phaeomelanin as in *Pongo pygmaeus*, the orangutan, or a black colour for eumelanin as in *Lemur macaco*, the black lemur The colouration of a hair is controlled by the deposition of either phaeo- or eumelanin as the hair grows. The agouti banding occurs when this process switches between the deposition of phaeomelanin to eumelanin as the hair grows, causing the typical banding pattern (Hershkovitz, 1977). The bleaching process occurs over evolution, changing the colour of the hair by a reduction in the deposition of either eumelanin or phaeomelanin. The bleaching process of a pelage may not be one continual progression from saturation, lightening to white. Hair colour can change from red (phaeomelanin) to white simultaneously. The cause can be environmental or genetic, which switches the function of the melanocyte from producing saturated phaeomelanin to none at all. The process of bleaching causes the greying of hair with age, as the melanocytes cease to produce melanin. The principle of metachromism was tested in tamarins by Jacobs *et al.* (1995) using phylogenetic relationships based on the mitochondrial DNA sequences of two genes. Sixteen areas of the pelage were examined

and compared for hair colouration, to identify the evolutionary trend of chromatic bleaching. The pattern described by Hershkovitz (1968) was identified in the genus *Saguinus* (13 species and sub-species), to give support for the altered expression of genetic variation by developmental constraints causing metachromism (Jacobs *et al.*, 1995).

The simultaneous agouti or bleaching process of all hairs creates a monochromatic pelage; the number of potential pelage patterns however, is massive. Each hair or group of hairs form a chromogenetic field that can produce pigmented colouration by switching on and off, or limiting melanin production (Hershkovitz, 1968). According to the theory of metachromism, the evolutionary fate of a species' pelage is white and monochromatic, as in the polar bear or albino animals. It is therefore unlikely that once a species becomes achromatic, it will ever gain colouration again without some genetic and environmental intervention. Machida and Perkins, described in Hershkovitz (1977), examined the distribution of melanocytes over the bodies of 48 primate species. Species were grouped into one of four categories to best describe the distribution of melanocytes; species which were heavily pigmented on the epidermis only (e.g., *Alouatta caraya*) or with light-moderate epidermis pigmentation (e.g., *Cebus apella*), species that show pigmentation only in the dermal region (e.g., *Papio sphinx*), species with pigmentation in both epidermal and dermal region (e.g., *Pongo pygmaeus*), and those with no pigmentation in the dermis or epidermis (e.g., *Erythrocebus patas*). Machida and Perkins predicted an evolutionary trend towards greater epidermal pigmentation. Hershkovitz (1977) disagreed with this conclusion, as the most "primitive" primates (i.e., strepsirhines) are not pigmented in either the epidermal or dermal region. Thus, pigmentation loss must be degenerative as the ancestral melanocytes were inherited from our chordate ancestors.

The origins of the agouti patterning may be associated with cryptic colouration, as it is generally the least visible pelage of animals (Jacobs *et al.*, 1995). Most nocturnal species also display the cryptic agouti pelage, which is the ancestral form of hair patterning, without the need to develop conspicuous stripes, spots and a bright colouration.

1.4 Sexual selection theories

Differences between the sexes are common in primates; the main morphological differences are weight and muscle development, body dimensions, pelage colouration and ornamentation, anatomical features (such as larger canines) and maturational or seasonal, periodic differences associated with reproduction (Crook, 1972). Darwin (1871) defined secondary sexual characteristics in terms of differences between the sexes that are not features of reproduction. These are differences in size, strength, weapons of offence or defence, vocal, colouration, and ornamentation. Darwin was the first to suggest the theory of sexual selection as an alternative to natural selection, defining sexual selection as "the advantages which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" (Darwin, 1871, p. 256). The evolution of secondary sexual differences necessary to gain an advantage over other males will be transmitted to the male offspring (Darwin, 1871). There are two forms sexual selection; intersexual selection, which evolves though mate choice for a characteristic, and intrasexual selection, which evolves due to direct competition for a mate. The secondary sexual character of interest to this study is pelage colouration (ornamentations and sexual size dimorphism are also considered).

There are many forms of competition between males for females, with the use of ornaments and bright pelage colourations being the more peaceful form by "exciting and charming" the females (Darwin, 1871, p. 297). Darwin describes brightness and colour as varying intraspecifically between sexes in many genera from insects, birds, fish, amphibians and reptiles to mammals, stating that ruminants display sexual differences in colour more than in any other mammalian order. Terrestrial carnivores and insectivores rarely exhibit any kind of sexual differences, unlike marine species such as fish, where sexual differences can be extreme (Darwin, 1871). Darwin concludes that adult males most often display the brightest colours as a result of sexual selection. There is evidence over an array of animal species for the phenomenon of a brightly coloured male and a dowdy looking female, extreme examples of which are presently in birds (e.g., the peacock). Diurnal primates are also good examples of this phenomenon with almost every family displaying at least one example of sexual dichromatism (see Appendix 1.8). In some species (e.g., *Eulemur fulvus rufus*, the red-fronted lemur) reversed sexual dimorphism exists, where females are brighter and more ornamented than males. Species that have brighter females are also commonly female dominant suggesting an association between a bright pelage and dominance.

Darwin vs. Wallace

Although Darwin had good support for his proposal that sexual selection produces secondary sexual characteristics, such as colouration and ornamentation differences between the sexes there were others who considered colouration and ornamentation differences between the sexes to be a product of natural selection. Wallace was Darwin's main opponent. He proposed that protection and recognition were reasons for the differences between the sexes in pelage colouration. Wallace argued that it was not the

male's bright colours which were being selected for, but a female's dull colouration (Cronin, 1991). The reason for a female's dowdy colouration was protective, as females play a more important role of reproduction. One example Wallace used was of a bird incubating eggs. It is primarily the female that performs this task and the drab colouration conceals the presence of the bird, and the nest, from the attention of predators. Wallace's second theory for a dimorphic pelage was the evolution of the bright male pelage for species recognition. He suggested that a bright pelage promoted efficient mating by helping animals to recognise the opposite sex and prevent inter-specific mating (Cronin, 1991).

Both theories could explain certain examples of species dichromatism, but not the most conspicuous colourations and the presence of flamboyant ornaments. Surely, the elaborate displays, which have high energetic cost, could not solely be a means of recognition. Wallace claimed the theory of sexual selection to be unnecessary and attempted to provide an explanation for the vivid colours seen in males. The theory of physiological conspicuous colourations was born, as a non-adaptationist view of the evolution of pelage dichromatism (Cronin, 1991). Wallace explained that all tissue and fluids are brightly coloured and organisms will tend to become multicoloured as a result of physiochemical changes. He suggested that the "natural" state of an organism would be polychromatic, if not subjected to natural selection. Wallace further suggested that colour increases with physiological activity. Therefore, colour would be more vigorous in males who are more active, causing bright pelages. The flamboyant colours, he explained, were caused by colours increasing in intensity and variety as external structures differentiate and change. This suggests that with the evolution of ornamentation, the evolution of bright colours should follow (Cronin, 1991).

The problem with the theory proposed by Wallace is it is non-adaptive and thus colouration has evolved due to physiological processes alone, which must be selectively neutral (Cronin, 1991). Despite support for the concepts of Wallace from scientists of his time, the physiological explanation for dichromatic species does not hold with his explanations of the dowdy female, as highlighted by Cronin (1991). According to the rules of inheritance, outlined by Darwin (1871) the colour differences could not be inherited by only one sex, if expressed in both sexes, as suggested by Wallace. Therefore natural selection alone cannot account for the protection and recognition theories for dull females if males were bright for physiological reasons. Both Wallace and Darwin propose theories that seem to favour one sex; Wallace's theories favour dull females and Darwin's favour bright males, each to exclusion of the adaptations of the other sex.

Mate choice

Modern evolutionary theory notes that sexual selection is caused by the competition between males for a mate, and the exertion of choice, usually by a female, for a mate. Sexual selection was defined by Halliday (1985, p. 4), as "any pattern of behaviour, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex, than with others". Both males and females exert choice in a mate with different benefits, both direct and indirect. These benefits are outlined by Andersson (1994): high fecundity, immediate gains and parental care, resources and high male status, male complementarity, good physical condition, and courtship displays.

Each benefit can be visualised and directly selected by the use of some cue that is interpreted by the "chooser" as a benefit and depends on the differential parental investment of each sex (Trivers, 1972). The benefits of males choosing a female will not

be considered here, as only female choice is of interest to this study. However, males do make informed choices for a mate; for example, males choosing larger females has a direct relationship with fecundity (Andersson, 1994).

The presence of sexual dichromatism may be related to mate choice by one sex (Halliday, 1985). The direct benefits of this exertion of choice are as follows; females choosing for high fertility in a male is often associated with the dominance of an individual, which is associated with male-male competition or sperm competition. For example, primates who live in multi-male groups, have a dominant alpha male who exerts dominance over sub-ordinates through aggression. A female may also exploit physical cues to the fertility of a male, such as colouration or other visual cues (Partridge and Harvey, 1986). Females may choose a male for parental care through the offer of food resources and territory (MØller, 1988). A male's high status will ensure the dominance over females in a harem or multi-male group in primates (Bernstein, 1976). There are often, however, extra-pair or "sneaky" copulations by a sub-ordinate member; therefore, dominance does not assure paternity (Halliday, 1985). Females usually choose a mate that is unrelated, which is a behavioural response to prevent inbreeding; for example in *Lemur catta* (ring-tailed lemur), females remain in the maternal group with males being forced to disperse before maturity (Tattersall, 1982). Females can also select males in good physical condition. A healthy appearance is a cue used to select for 'good genes' by phenotypic expression, such as a bright pelage, which may be influenced genotypically by the health or susceptibility of an individual to parasitism (discussed below).

There are presently several theories concerning sexual selection for the evolution of

secondary characteristics (sexual dichromatism and ornamentation) outlined by Partridge and Harvey (1986):

1. Species specific ornaments evolved (in birds) to prevent individuals from mating with individuals of other species.
2. Females choose mates by their ornaments because they indicate viability that will be transmitted to offspring.
3. Male ornaments impair survival and have evolved through female choice (Handicap hypothesis) Zahavi (1975).

The first of these theories will not be considered in depth, as it is based on observations on birds and is not relevant to this study. Considering mate choice within the realms of sexual selection, there are two main theories to explain the evolution of ornamentation and sexual dichromatism. These hypotheses will be discussed with the experimental evidence. The first hypothesis was suggested by Darwin (1871) and has been coined as the "good taste" hypothesis, whereby females choose males for their beauty. The presence of ornaments and conspicuous colours may hamper a male's survival, but the costs are outweighed by the increase in reproduction, due to female choice for the trait. Darwin continues by explaining that this burden on the male could not threaten a species survival due to the process of natural selection, which would remove the most excessive deleterious ornaments and colours. Wallace suggested the converse hypothesis; females choose males for their vitality, health or stamina which are signalled by the presence of colours and ornaments (Cronin, 1991). He continues by using the theory of natural selection to explain how the brightest males may not be the fittest, these males would not survive and so the trait would be selected against. This hypothesis is known as the "good

sense" hypothesis. It is considered to be an adaptive choice for a mate and the "good taste" hypothesis as non- or maladaptive (Cronin, 1991).

The "good sense" hypothesis is of interest to this study. There are several more theories, which support the "good sense" hypothesis of Wallace. These theories are termed "good genes" and the handicap principal. There are also several further satellite theories that stem from the "good sense" hypothesis. The first theory is the "good genes" hypothesis, which explains females choosing mates for their secondary sexual characteristics as a selection for viability. It is concerned with the heritability of fitness (Partridge and Harvey, 1986). According to population genetics, a population which is at equilibrium and subject to natural selection is not expected to exhibit "total fitness heritability" (Kirkpatrick, 1982). It also predicts that when there is a balanced polymorphism for a selected trait, there will be no heritability of fitness (Maynard Smith, 1976). This means that there cannot be an individual with better genes for a given trait. If both genetic theories are considered to be true, then the exertion of female choice could have no effect on the fitness of the offspring. Therefore, how can the phenomenon of non-random mating be explained? Parker (1985) suggests that most mate selection, such as that based upon a bright colouration, results in only phenotypic benefits. To overcome this problem of 'good genes' selection, Partridge (1985) suggests the stale-mate could be overcome by the temporal cycling of selection pressures (e.g., females choosing the rarest male phenotype) (Lewontin, 1974). The interaction of variables that affect selection could also allow for fitness heritability, such as mutation (Partridge, 1985).

Darwin's "good taste" hypothesis was considered by Wallace to be lacking an explanation for female choice. The adaptive element was provided by Fisher (1930). He

stated that choosing an attractive (by colouration or ornaments) male, for a mate is adaptive for a female, as the male's offspring will also be attractive. Hence, there will be a higher reproductive potential through female choice for the trait. The trait which the female chooses will be based on the "fashion" of female choice and will be maintained in the next generation by female offspring choosing the same trait as their mother (Fisher, 1930). The spread of choice for a particular feature is explained by inheritable preference and the feature gene. The male feature gene will be expressed phenotypically for colouration and ornamentation and by the preference of the feature by females. Therefore this process is selective and frequency dependent, where most females choose males with a similar feature, such as pelage colouration. The evolution of this feature has been termed the "runaway" hypothesis, as there is a positive feedback between female preference and male display (Krebs and Davies, 1993). The problem is in explaining how the Fisher process is started, which seems to require some type of good genes model.

Many experiments have been used to test the "good genes" hypotheses, which are generally divided into the handicap model (Zahavi, 1975), and condition dependent handicaps (Krebs and Davis, 1993). Zahavi suggested that females were choosing males for their ornaments and bright colours because they are a handicap to the male (Zahavi, 1975). The ability of the male to cope with the handicap acts as a signal of genetic quality to the female; the more debilitating the handicap, the better the male's genes for coping with the handicap, due to the male's survival. Both Darwin and Fisher have claimed that secondary sexual characteristics would reduce the survival of the male. This survival quality caused by the handicap pertains to a male's reproduction and survival and not, as in Fisher (1930), solely as a function of attractiveness to females. Zahavi claims that females are considering the costs of an ornament or colour to the male, when

making a mate choice. In theory, the cost of an ornament could be mimicked by males who had genes that were superfluous to survival. Zahavi also suggests that dishonest advertising would not be evolutionarily stable and would lead to the evolution of characters that could not be faked (Cronin, 1991). One of the main criticisms of the handicap hypotheses is that if all males must bear the same handicap at an energetic cost with an inflexibility of the trait (Krebs and Davis, 1993), there probably is no genetic linkage between the marker of quality and the marker of the individual (Zahavi, 1975). Handicaps must be condition dependent or flexible in their appearance so that the degree of expression of the handicap indicates the male genetic quality (Krebs and Davis, 1993). This makes the handicap principal similar to the "good genes" hypothesis.

Currently the most popular variant of the "good genes" theory is the Hamilton-Zuk hypothesis, which relates the brightness of an individual's plumage to its susceptibility to parasitism (Hamilton and Zuk, 1982), discussed below. Other research concerned with non-random mating and fitness heritability concern a range of genotypes associated with phenotypes of ornamentation and colouration; for example, females choosing mates for parental ability with respect to their plumage. Sundberg and Larsson (1994) investigated the monogamous yellow hammer, *Emberiza citrinella*, which exhibits bi-parental care, as the male helps feed the young. Despite practising monogamy, it was shown that variation in male parental care increases variation in reproductive success (Price, 1984). Colour, attributed to various body parts of males was not associated with feeding rate, but correlated with fledging number, indicating parental quality. Comb size and colour also were found to correlate with the physical condition of the red jungle fowl, *Gallus gallus* (Ligon *et al.*, 1990). The most physically fit individuals were also found to be the most successful in male-male competition. Blood testosterone levels were shown to correlate

with a male's health, comb size and colour. Both are examples appropriate to Darwin and Fishers "good genes" hypothesis of females choosing the "best" male for a specific trait that is expressed phenotypically using ornamentation and colour.

Genetic modelling has been applied to the concept of the handicap hypothesis to test it as a mechanism for the evolution of secondary sexual characters. Models of mortality associated with the size of an ornament using quantitative genetic models were developed by Maynard Smith (1976) and Lande (1980), to identify how ornaments could spread via sexual selection (Andersson, 1982). This method provided a model for the handicap hypothesis to show how ornaments could act as an index of fitness through female choice. Kirkpatrick is among many scientists (e.g., Bell, 1978; Davis and O'Donald, 1975) who do not believe in the handicap method of sexual selection. In his paper entitled "The handicap method of sexual selection does not work", he used genetic modelling to demonstrate the theory was unsupported (Kirkpatrick, 1986). Three characteristics were included that are related to the handicap hypothesis: male handicap, female preference for a handicap, and a viability trait. Kirkpatrick found that in species that do not contribute materially for the offspring, female preference is arbitrary and yet could still result in the evolution of secondary sexual characters.

Sexual selection theory is composed of several schools of thought as to how differences in extravagant ornaments or colours have evolved between the sexes. These are the conditions that affect the quality of the trait and the feature that a female is selecting for from a mate. Zahavi has suggested a new alternative to sexual selection theory with regards to the evolution of secondary sexual characteristics. Secondary sexual characteristics were displayed as an "adaptive signal of extravagance" (Zahavi, 1990, p.

501). The evolution of each signal was the same as the evolution of mate choice. Therefore, the signal can be used in determining rivals during male-male competition. He termed the selection force as signal selection, which can be applied to all signals of extravagance outside of the realms of reproduction, such as the evolution of cryptic colourations. He also stated that the investment in the signal is often more than required to transmit the message, making many signals energetically wasteful (with regards to ornaments and colours as signals). Such particularly wasteful signals he claims, would not have evolved through natural selection (Zahavi, 1990).

1.5 The Hamilton-Zuk hypothesis and intraspecific variation

The question to be asked is why would females choose to mate with the brightest coloured males. The theory that females are duller than males for protection and camouflage was discounted by Darwin when considering that the dullness of the female did not differ in a sufficient degree from the male to afford the female protection. He suggested that bright colours in males must be beneficial in rivalry with other males but could not deduce why. The idea that females choosing bright males for mates as an index of potential genetic quality has been considered (Smith, 1978). The theory that a condition dependent handicap exists as a means of determining health, seems a better explanation for the handicap hypothesis, where the handicap is a fixed trait, but until Hamilton and Zuk's paper in 1982, this theory was not given a specific mechanism.

Hamilton and Zuk suggested the hypothesis that heritable fitness in birds in relation to parasite susceptibility could be determined by a female using the brightness of a male's

plumage. Females select genes for resistance to pathogens and parasites that would affect the heritable fitness of an individual. The appearance of a pelage or plumage is affected by the health of an individual by becoming dull, bald, or matted, often caused by a reduction in the preening or grooming of an individual when unwell. The Hamilton and Zuk (1982) hypothesis is an extension of this observation with a heritable trait for pelage/plumage brightness. There are two main elements to the hypothesis:

1. Animals showing more strongly developed characters would be expected to be subject to a variety of parasites (except for acute pathogens).
2. In species where disease is relatively unimportant or only acute diseases occur, mate choice should be less apparent and so the animal less showy.

From these two statements, Hamilton and Zuk inferred that evidence of sexual selection should be present in species with a wide range of parasites, as one sex chooses individuals with the fewest parasites and the highest resistance. Over a series of seven surveys of blood parasites on 7649 individuals from 109 passerine bird species, plumage brightness was scored using a visual rank of 1-6, 1 being dull and 6 very striking. Male song was also scored on complexity. Results showed a positive correlation between low parasite number and "showiness" of pelage in males interspecifically. They concluded there was weak evidence for mates choosing individuals for genetic resistance using scrutiny of characters whose full expression is dependent on health and vigour.

After the initial study, the question became whether this mechanism was real or just a product of common descent, as phylogenetic associations had not been accounted for. The test was repeated with Hamilton and Zuk's original data, including data on

European passerines. The effects of taxonomic behavioural and ecological variables were removed using randomisation tests for every genus by calculating the intra-generic rank correlations of continuous variables (Read, 1987). Read demonstrated that parasite prevalence and male brightness positively correlated across a species when the confounding variables were removed, and that parasite prevalence and brightness correlated within genera, showing the association has arisen many times through evolution. Read continued testing the Hamilton Zuk hypothesis by repeating the tests on the original data independently scoring the "showiness" of individual birds (Read and Harvey, 1989). It was demonstrated that the relationship between male brightness and haematozoan prevalence only existed in species where few individuals had been sampled.

A further comparative study was performed by Zuk (1989) on haematozoa from 256 species of tropical Central and South American birds. Both male and female brightness (but females less so than males) were associated with parasite load, but only in resident species (there was no association in migrant bird species). Sexual dichromatism was not related to parasite level in migrant or resident species. Phylogenetic associations were examined and controlled for using the combined *p*-value test and a consensus test. Zuk suggests the reason for only slight brightness differences between males and females being associated with parasite prevalence could be limited by a species' developmental genetic constraints. It could also be limited by increasing parasite pressure, increasing selection on discrimination between sexes reducing sexual appearance differences. It has been suggested that both sexual and natural selection may work differentially on each sex to confound interpretation based on mate choice alone (Read, 1991). Read continued to pursue the evolutionary role of parasites and sexual selection with the association of polygyny in passerines, suggesting that polygynous species are more resistant to

haematozoan infection, resulting in resistant males (Read, 1991). The role of parasites in passerines is also considered to have an effect on the evolution of sexual size dimorphism (Potti and Merino, 1996). The authors showed that the detrimental effects of ectoparasites on individuals was greater in males, and proposed that "parasites may interact with both host hormones and the host immune system to cause sexual size dimorphism in young animals" (Potti and Merino, 1996, p. 9).

Intraspecific methods also have been employed to test the Hamilton-Zuk hypothesis. The role of female choice, male ornamentation, and endoparasitic load has been studied in the wild turkey, *Meleagris gallopavo* (Bucholz, 1995). Snood and skull-cap size was shown to determine a female's preference for a mate. Oocytes (parasite eggs) counted from the faeces of wild caught males were negatively correlated with female choice, providing support for the Hamilton-Zuk hypothesis. Limited support for the hypothesis has also been found in male satin bowerbirds (*Ptilonorhynchus violaceus*), showing an inverse correlation between the ectoparasite *Mysidea ptilonorhynchi*, and mating success (Borgia and Collis, 1989). They found further support for the hypothesis by demonstrating that an individual's ectoparasite infection did not significantly change over time, and that older males had fewer parasites than young males. No relationship however, was found between ectoparasite load and plumage quality. Similarly haemoparasitic infection in 97 Redpoll finches (*Cardius flammea*) showed no association with plumage redness in males (Seutin, 1994). MØller has concentrated on using the monogamous barn swallow (*Hirundo rustica*) as a model by examining the ectoparasite (*Ornithonyssus bursa*), most commonly found on the birds and in the nests. He had determined previously that mated males most commonly had longer tails (MØller, 1988).

He then showed that mated males had significantly fewer mites than unpaired males, which negatively correlated with tail length (MØller, 1990a). This work illustrates that females are selecting for male fitness, and was further supported by the finding that chick survival rate was significantly reduced with an increase in mite number (MØller, 1990b).

Alternative research concerned with the Hamilton-Zuk hypothesis considers species other than birds, to identify if the parasite/colouration phenomenon is particular only to bird species or applicable to other species. The majority of the studies use fish as the subject, with guppies and sticklebacks being most common, due to the red spots formed from carotenoids, which are found on males' backs during the mating season. A study on the three-spined stickleback (*Gasterosteus aculeatus*) showed some support for the Hamilton-Zuk hypothesis, by demonstrating that the intensity of the male red colourations were positively correlated with physical condition (Milinski and Bakker, 1990). Males who were heavily parasitised had a duller red colouration, and females consistently chose males displaying the brightest red under various lighting conditions; demonstrating female choice for the healthiest mates and possibly also for parasite resistance. Another model considers bright areas of pigmentation caused by carotenoids, in the guppy, *Poecilia reticulata*. These spots are an intense orange colour usually found with black spots (melanin), and some iridescence (not found in all individuals), which have been shown to be attractive to females (Endler, 1980). Females choose mates with the more intense orange colourations (Brooks and Caithness, 1995a). The intensity of orange is obtained through a high carotenoid diet and this is a condition dependent trait (Kodric-Brown, 1993; Brooks and Caithness, 1995a). It should be noted that in farmed fish, food that is provided is already high in carotenoids and therefore, would not be an

accurate indicator of health or foraging ability compared to wild fish. It has been demonstrated that females also choose a mate dependent on the symmetry of the spots. Females choose the most symmetrically patterned male as well as considering the brightness of the spots (Sheridan and Pomiankowski, 1997). There was a large fluctuation in the symmetry of melanic spots, but the orange spots were highly symmetrical and conserved. It would appear that not only the brightness of a colour is important to female choice, but the area and nature of the pattern (Brooks and Caithness, 1995b; Sheridan and Pomiankowski, 1997). A significant correlation was shown in 27 species of freshwater fish, between sexual dichromatism and the number of parasite genera (Ward, 1988). Sexual dichromatism was found to be more marked in males at the breeding season, suggesting a relationship with sexual selection. Both findings provide support for the parasite resistant male Hamilton-Zuk hypothesis.

Despite the majority of the studies testing the Hamilton-Zuk hypothesis involve birds or fish (no mammals have yet been considered), a few amphibians and insects have been studied. It was shown that female crickets from two species (*Gryullus veletis and G. pennsylvanicus*) preferentially selected old males (Zuk 1987a), which also correlated with the number of gregarines (sporozoan endoparasites) found in the gut (Zuk, 1988). There was no selection for body size by the females, colouration was not tested (Zuk, 1988). Older males which were less parasitised were able to produce more spermatophores, which could also be linked to reproductive success, suggesting females selecting for health and reproductive viability of mates (Zuk, 1987b). These bright colourations and ornaments appear to be frequently selected traits used in choosing a mate, where females select for secondary sexual characteristics in males. The brightness of a colour, or the flamboyance of an ornament can advertise several traits: health and

parasite resistance (Hamilton and Zuk, 1982; Zuk, 1988, 1989; Read, 1987; MØller, 1988; Borgia and Collis, 1989; Milinski and Bakker, 1990; Bucholz, 1995), parental abilities (Sundberg and Larsson, 1994), reproductive viability (Zuk, 1987b), and condition dependent on foraging ability trait (Kodric-Brown, 1993; Brooks and Caithness, 1995a; Bortolotti *et al.*, 1996). In all cases females are using the principles of sexual selection to ensure healthy, viable offspring, and this choice maintains the evolution and persistence of secondary sexual characteristics such as a bright colouration and ornamentations.

1.6 Primates and their parasites

There are around 150 parasites which can affect primates, infecting the digestive tract, the liver, the circulatory system, the respiratory system, urinary system, skin and subcutaneous tissues (Soulsby, 1968). The groups of parasites affecting primates (including humans) are trematodes, cestodes, nematodes, protozoans, leeches, and even arthropods. The most common parasite found in primates are the helminths which includes the nematodes, trematodes and cestodes (Ruch, 1959). Nematodes are roundworms that are cylindrical in shape, where the female is larger than the male. The worms vary in size from 0.5mm to 35cm (Ash and Orihel, 1987). The trematodes are flukes that use aquatic snails as intermediate hosts with invertebrates or vertebrates as second hosts (Ash and Orihel, 1987). The most common cause of trematode infection is from ingestion via contaminated food (Thienpont *et al.*, 1986). Cestodes are tapeworms that can grow to be meters long and are most commonly ingested in infected meat or fish

(Ash and Orihel, 1987).

The parasites that are of interest here are endoparasites that spend some part of the lifecycle in the gut. Analysis of the presence of these parasites involves collection of faecal material and microscopic examination of the material for oocytes (eggs), worms and larvae. The collection of parasite data from faeces is a good method of assessing the health, diet and even social status of the animal (Stuart and Strier, 1995). The first use of parasite load data from primate faeces was by Hausfater and Watson (1976). The study involved collecting parasite data of oocytes from baboons (*Papio cyanocephalus*) in the Amboseli National Park, Kenya. They found a correlation between high egg emissions and the dominance of males. Female parasite loads were higher than the males but did not correlate with rank. However, sexually cycling females had the highest parasite loads. It was suggested that this may correlate with a higher rate of food ingestion. The alternative suggestion was that dominant males and sexually cycling females could provide a more favourable internal environment for proliferation of endoparasites.

The definition of a successful parasite is one which becomes so adapted to the host and the host to it that the host is not harmed by the parasite (Fiennes, 1967). Parasites are usually specific to a host species found in a known habitat. When populations of primates are moved into other habitats with other primate species, the parasites may be incorporated into other species and adapt to new hosts (Stuart and Strier, 1995). It has been shown that the susceptibility of a species to parasitism is dependent on moist and humid conditions (McGrew *et al.*, 1989). Conversely, an arid environment may also lead to an increase in susceptibility to water-borne parasites, due to the infection of limited water sources (Stuart and Strier, 1995). There should also be a relationship between

primate population densities and transmission of parasites through the group, although a study by Stuart *et al.* (1993) showed the contrary with low population densities of muriquis having high levels of parasites. High parasite loads in individuals can have an effect on a primate's behaviour by avoidance of transmission through choice of mate (Hamilton and Zuk, 1982), avoidance of sleeping areas at times of high transmission risk (Hausfater and Meade, 1982) and avoidance of contaminated foraging routes (Stuart *et al.*, 1990).

A large comparative study was conducted by Bush *et al.* (1990) in which parasite data on 582 host species was gathered from 1222 studies for a range of vertebrates: fish, herptiles (amphibians and reptiles), birds and mammals (only one primate, *Alouatta caraya* was included). The richness of gut helminths in the vertebrate groups was compared between terrestrial and aquatic habitats to determine the "evolutionary age" due to phylogenetic differences. This theory is termed the "time hypothesis" where phylogenetically "older" groups such as fish should have greater parasite species richness than "younger" groups such as the mammals. The fish and herptiles had lower numbers of parasites than the other groups, showing no support for the "time hypothesis". The tests were repeated on helminth richness using some of the data from Bush *et al.*, (1990) and some newer parasite studies totalling over 400 data sets (Gregory *et al.*, 1996). Tests were also repeated adjusting for phylogeny using the Felsenstein method of comparison, which is designed to control for the effects of phylogenetic associations using differences at daughter nodes (Harvey and Pagel, 1991). The results showed a tendency for aquatic species to harbour more parasites, which was contradictory to the results of Bush *et al.* (1990). A positive correlation with body size was also shown, which was explained by niche availability, rate of parasite acquisition, host population dynamics, species-area

analogy and the evolution of parasite and host (Gregory *et al.*, 1996). There appears to be a close association between the evolution of the host and parasite, which could also account for possible correlation's between a primate species' or individual's behaviour and parasite load.

1.7 Natal colouration theories

Darwin's definition of a sexually selected pelage was one that would not be apparent until maturity (Darwin, 1871). This case does not apply to the colouration some infants possess in the early stage of life. He was the first to note that pelage colouration can vary ontogenetically and described six cases of variation in pelage colour development (Darwin, 1871). Although attributed to bird colourations, four of the cases apply to primates. The first case describes species where sexual dichromatism is present in adults, with males having a brighter pelage. Infants in this type resemble the adult female in pelage colouration; for example, *Hylobates hoolock*, the hoolock gibbon, displays sexual dichromatism where the males are black and the females and infants buff in colour. The second case is when there is sexual dichromatism, the female is more conspicuous in colouration; here the infantile colouration resembles the male (e.g., *Eulemur fulvus rufus*, the red-brown lemur, has grey males, red-brown females and grey infants). The langurs are good representatives of the third case outlined by Darwin, where there is no sexual dichromatism, but there is a natal colouration. *Trachypithecus cristata*, the silver leaf monkey, has dark grey adults of both sexes and bright orange infants. The fourth case is the most common in primates, where there is no variation in pelage colouration with age or sex, as in *Macaca silenus* (the lion tailed macaque) the species is black, with

a golden-grey ruff surrounding the face at all ages. Darwin stated that each case depends on the transmission of genes between the sexes and the forces of sexual selection on adult pelage colouration.

The theory of delayed pelage maturation (Andersson, 1994) despite being based on observations in birds, can also be applied to primate colouration, particularly to the case of a natal pelage. The theory describes the timing of the development of an adult pelage as sexually selected. This would apply to cases one and two described above, where sexual dichromatism is present. The presence of a natal colouration is a consequence of the adult colouration not developing until maturity. Three hypotheses have been proposed for the occurrence of delayed pelage maturation. The "crypsis hypothesis" states that the risk of a male infant displaying mating colours would be too great, due to male aggressive displays in competing for females (Selander, 1965). The "female mimicry hypothesis", states that a female colouration in infants is a less threatening colouration to adult males (Rohwer *et al.*, 1980). The "status signalling hypothesis" states the natal pelage is a signal of subordinance to adult males (Rohwer, 1977). There are primates that display both natal colouration and sexual dichromatism, for example *Hylobates concolor* and *H. hoolock,* to whom all three theories could apply.

None of the theories mentioned provide a reason for the evolution of natal colouration independent from sexual dichromatism, in cases when adults are similar but there is still a natal pelage. Primate infants are in an altricial state, where the degree of infant care is a major correlate of infant survival (O'Brien and Robinson, 1991). A common feature of mammals is the presence of an age-specific pelage with regards to texture, thickness and colour (Hershkovitz, 1977). If this is such a common feature, the presence of a natal

coat must have a specific function. There are three major factors that contribute to a primate infant's survival (Chance and Jolly, 1970):

1. The processes of maturation in the infant, which include not only maturation of physical ability and skill, but also concomitant changes in its behaviour.
2. Changes in the behaviour of the mother.
3. The amount and diversity of social relationships which the infant experiences.

A combination of these factors could be associated with the evolution of natal colouration in primates. Suggestions for the display of a natal coat in primates are many and varied. Infants of many species are clearly marked; in many primates, the natal coat is of a different colour to the adults (Jolly, 1972). It has been suggested that skin and coat colours distinguish an infant from other group members (Swartz and Rosenblum, 1981). These defining features disappear at the developmental stage when an infant can locate and identify the mother. This stage is usually between 2-3 months (Poirier, 1970).

Several general theories for the evolution of a natal pelage have been described. The first is related to the vulnerability of the infant, whose survival is solely dependent on the mother and the reaction of conspecifics towards it. These age-specific characteristics could distinguish dependent infants from older, relatively independent individuals (Alley, 1980). Alley states three reasons for the need of social animals to detect the age of conspecifics:

1. The young must be recognised for caretakers to be able to provide them with the requisite protection and care

2. Adults must recognise those young that are not yet old enough to fend for themselves, so caregivers can reassure their investments of protection and care for this age group
3. Older individuals should be encouraged to be less dependent and leave their parents

An infant's pelage acts as a visual stimulus that is important in the evocation of behaviour (Struhsaker, 1971). A behaviour can be said to have a function if it can be shown that within the organism's natural environment, it contributes to the individual's reproductive success (Symons, 1978). If a behaviour has a function, it is to say it has been shaped and sculpted by natural selection (Symons, 1978). Does natal colouration therefore have a function, and if so, is it influenced by natural selection and not, as for sexual dichromatism, by sexual selection?

Two forms of behaviour must be considered with respect to the need for a natal coat, that of the mother and of the other group members towards an infant. The natal pelage has been hypothesised as an essential element in releasing a female's maternal behaviour, as it coincides with the period of maximum dependency (Poirier, 1970). Poirier showed there was a positive correlation between the natal coat colour of an infant and the protracted concern of females. Others also consider the function of a natal coat to invoke the release of maternal instinct (e.g., Jay, 1963) and Crook (1971) considers the natal coat to be linked to a genetically programmed care response in females. Not only the mother is interested in the infant, in some species so are all females in the group (Jay, 1963). This might indicate that the behaviour is stimulated visually by the display of a coloured natal pelage. The presence of a distinct natal pelage also could relate to

pronounced infant sharing, which draws females to care for the infant (Jolly, 1985). Infant caretaking is commonly known as allomothering or allocare, where females other than the mother share in the responsibility of caring for an infant. The relationship between the presence of a natal coat and allocare was proposed by Hrdy (1979). She suggested that the flamboyant coats seen in many colobines act to promote care by group members other than the mother. The natal coats found in langurs (the colobines referred to), differ dramatically from those of conspecific adults and this is considered to be a colobine hallmark. These seemingly flamboyant coats are hypothesised to instil postnatal transfer (Blaffer-Hrdy, 1980). Other theories concerned with the allomothering of infants suggest that it is for reciprocal benefits to both the carer and the mother (Fairbanks, 1990), allowing the development of skills from other carers (Quiatt, 1969), altruistic reasons (Stanford, 1992), rewarded by grooming (Muroyama, 1994), mothering practice in young females (Lancaster, 1972), enhanced status (Cheney, 1978; Gould and Gould, 1989), or kin benefits (McKenna, 1979).

Allomothering is found in many primates, some of which do not possess a natal colouration (e.g., ring-tailed lemurs and capuchins). All infantile characteristics in primates may act as cues to elicit care-taking behaviour (Alley, 1980). A comparative study was used to compare allomothering behaviour with the presence of natal colouration in primates (Treves, 1997). It was shown that there was a correlation between allocare behaviour and the presence of a natal coat. This study, however, did not control for phylogenetic non-independence, which is essential when making comparisons between species (Harvey and Pagel, 1991). Another study compared the degree of allomothering with the possession and brightness of a natal coat with phylogenetic adjustments (Ross and Regan, in press). Only weak support was found for

the association between a natal pelage and the degree of allocare after phylogenetic adjustment *contra* Treves (1997). However, correlations were found between the reflectance of an infant's crown, leg and overall pelage colour with a high degree of allocare (Ross and Regan, in press).

Allocare has also been found to occur in the males of some primate species, such as *Macaca sylvanus* (the barbary macaque) where there is no natal colour present to instil this behaviour. Males may care for infants to regulate relations with other males, to increase access to mothers, and as part of their paternal investment (Paul *et al.*, 1996). In langurs, the adult males show no interest in infants (Poirier, 1970), despite their displaying a conspicuous natal coat. Old World primates practice allocare more often as they are often uni-parous, with long birth intervals (Alley, 1980). Allocare is much more common in colobines than in the cercopithecines, whereas the allocare exhibited in cercopithecines is more for the older infants (McKenna, 1979). Male allocare is practised in *Callicebus* spp. and the callitrichids, which are monogamous. This male allocare could be used to gain mating preferences from the females (Whiten, 1987). The distribution of male allocare does not seem to correspond with the presence of a natal pelage.

Another major theory for the possession of a natal coat is associated with the role of males. In multi-male or single male groups, there is often one dominant male living in a polygynous society with females and infants. Male aggression towards infants is common and the phenomenon of infanticide has a wide distribution of occurrence across the primates (Hrdy, 1979). Infanticide can have severe effects on the population (Blaffer-Hrdy *et al.*, 1995). A correlation was shown between the presence of a natal pelage and the aggressiveness of cercopithecine species (Booth, 1962). It was determined that the

pelage allows the young to be recognised,to reduce the risk of aggressiveness being shown towards the infant. In hamadryas baboons, there was an increase in the aggression shown towards infants, as their natal pelage changed to the adult colouration (Alley, 1980). Hair tufts, located on the rump in young chimps and gorillas as a white tuft, and a dark tuft on the head in rhesus monkey infants are considered to signal age and vulnerability in the infants. This should improve the tolerance of males and females (Alley, 1980). The role of males has contributed to two theories for natal colouration: a) infant defence, which predicts that take-overs, characteristic of single male groups lead to the selection for natal coats (Treves, 1997) and b) a theory described as paternity cloak, which predicts that the promiscuity characteristic of multi-male groups leads to the selection for a natal coat (Treves, 1997). Treves determines that there is no clear difference between the two hypotheses, providing only partial support for both. If a natal coat has evolved to reduce the risk of infanticide, it does not provide the ultimate protection. Infants with natal coats are frequently killed in instances when a new male takes control of the group (Alley, 1980). There may not even be a relationship between infanticide, allocare and natal colouration. For example *Colobus guereza*, black and white colobus monkeys, are infanticidal and yet undertake allocare duties, whereas langur males show no interest in infants and are infanticidal. The natal coat therefore, may inhibit aggressive tendencies but have no effect when there is a male leader take-over (Hrdy, 1980). A natal pelage seems to afford some protection in baboons, when a natal coat was visible there was a reduction in aggression shown towards the infant (Rowell, 1972). This changed to aggressive behaviour from 1-6 months as the pelage became progressively more adult-like in colour.

A natal pelage causes considerable interest in the new-born infants from the rest of the

group, to the point of forming grooming clusters around the infant (Washburn and Devore, 1963). Larger males often take no interest in the infants but, in some species, the males act protectively towards them. Male savannah baboons, *Papio hamadryas*, protect the young by surrounding the females with infants in rank order, with the most dominant male closest to the group (Chance and Jolly, 1970). The natal coat is said to mark the infants for more tolerance and protection (Altmann, 1980). Arboreal colobine infants are described as extra-attractive to other group members. The relaxation in predation pressure has given arboreal colobines a certain leeway in evolving conspicuous natal coats (Hrdy, 1970). The more terrestrial the species, the more vulnerable the infants who display a conspicuous coat (Hrdy, 1970). Terrestrial colobines do have more discrete natal coats; the partial terrestrial infants of *Nasalis larvatus*, the proboscis monkey, have a bright blue face, but a similar discrete adult pelage. Hrdy seems to assume that arboreal species are less vulnerable to predators than terrestrial primates. This may not be true, however, as many arboreal primates are smaller and therefore could be susceptible to a greater number of predators (e.g., eagles). A comparative analysis was conducted between predation rate, terrestriality and the degree of natal colouration in primates (Ross and Regan, in press). There was no correlation between a low predation rate and the possession of a conspicuous natal coat. It was also demonstrated that terrestrial primate infants display a less reflectant, but contrasting coat to that of the adult, which could still have some relation with predation risk (Ross and Regan, in press). No other studies have tried to test this theory, but it can be assumed that the benefits of a bright natal coat must outweigh the increased risk of predation pressure (Alley, 1980).

To summarise, there are various theories associated with natal colouration, most of which have never been statistically tested or analysed, to account for similarities between

closely related species (e.g., Treves, 1997). Many of the theories are the basis for hypotheses that are to be tested in this study concerning natal colouration and are listed at the end of this chapter. To summarise natal colouration could have evolved to: instil maternal instinct (Jay, 1963; Crook, 1972; Poirier, 1970), differentiate it ontogenetically from older members (Jolly, 1972; Swartz and Rosenblum, 1981; Hershkowitz, 1977; Alley, 1980; Struhsaker, 1971), stimulate allocare and infant sharing (Jolly, 1985; Hrdy, 1979; Alley, 1980), draw attention to the infant (Napier, 1970; Kavanagh, 1983), reduce aggression (Rowell, 1972), or to act as a form of protection (Altmann, 1980).

1.8 The Comparative method

The comparative method is frequently used by evolutionary biologists to study the adaptive fit between organism and environment. Over the last decade, there has been a revolution in the use of the comparative method by the development of various tests enabling across species analyses taking account of the fact that species are not independent data points. It is now possible to consider the results of recent comparative analyses to be comparable with experimental results, in terms of credibility (Harvey and Pagel, 1991).

Phylogeny and evolution

A phylogeny is a genealogical history of a group, hypothesising ancestor-descendant relationships (Levinton, cited in Harvey and Pagel, 1991). The relationships of species both past and present are grouped into the form of a phylogenetic tree based on character similarities and differences. Branches radiate between species or sub-species

with the length of the branch corresponding to evolutionary time and distance. Extant species are at the tips of branches and extinct or ancestral species are nearer the root of the phylogenetic tree. Closely related species can be more similar than distantly related species in morphology, behaviour and ecology (Harvey and Pagel, 1991). Therefore, species that are closely related will share many characters through the process of identity by descent (i.e., passed down the generations from ancestral species). There are two other processes by which species can share characteristics, that of convergent or parallel evolution. A phylogeny can be constructed either taxonomically or phenetically. Taxonomists more frequently use characters that are identical by descent, pheneticists more frequently use the principle of phenotypic similarities that have evolved convergently or divergently (Harvey and Pagel, 1991). Phylogenetic trees are constructed based upon many types of characters. Trees are often constructed to be parsimonious (to minimise the number of evolutionary changes), but these are not always considered to be the best (Harvey and Pagel, 1991). However, if the rate of change of a character is small or sufficiently equal in different lineages, methods of parsimony in constructing a phylogenetic tree are justified (Felsenstein, 1983).

As the order Primates is composed of approximately two hundred species, constructing a definitive phylogeny for the order is very difficult. There are ever changing ideas on the relationships between species, and of the many methods that can be used to assess a phylogeny. The two main problems in estimating a phylogeny have been outlined by Purvis (1995). The first problem is that a strict consensus tree will lose its resolution, when only estimates are added. This is a large problem, as there are species discrepancies for the nomenclature, status and phylogeny in the primate taxa, such as the tarsiers (Niemitz, 1994). The second problem is to alleviate discrepancies of how species are distributed throughout the phylogeny. Both problems are unresolvable, but matrix

representation with parsimony can be modified to eliminate potentially redundant information when estimating a phylogeny.

Purvis (1995) constructed the primate phylogeny used in this study. It contains 203 species and was compiled using information from many sources, including maximum likelihood trees, cladistic or compatibility analyses, neighbour-joining trees, trees based on molecular data, phenograms, trees based on non-cladistic analyses of morphological and behavioural characters and taxonomies. Purvis has re-coded the source trees into a binary character matrix where:

1 = score taxa in the clade defined by the node

0 = score taxa in the sister clade

? = other taxa and missing taxa

These 112 source trees were analysed using a branch and bound algorithm on monophyletic nested pieces to compile the phylogeny.

CAIC (Purvis and Rambaut (1995), is designed to deal with the non-independence of data points that can create false patterns and mask real patterns. This is a major problem when making comparisons across species, as the closer relatives are more similar, sharing more characteristics than would be expected by chance. The programme CAIC uses Felsenstein's principles of phylogenetically independent comparisons with modifications as recommended by Burt, and Pagel (see Harvey and Pagel, 1991), and Purvis and Rambaut (1995). The test proposed by Felsenstein (1985) allows pairs of taxa that share a common ancestor to be compared. The variation between species is split into independent components with the same expected variance, and the evolution of

characters is modelled as a Brownian motion process (Purvis and Rambaut, 1995). Variance therefore accumulates linearly with time, allowing the estimation of values of nodes from the phenotypes of the descendants. Felsenstein (1985) allows comparisons between direct descendants to be made for each node with n-1 independent contrasts for n species. Purvis and Rambaut (1995) state that the Felsenstein method is limited as it assumes that polytomies (more than two secondary branches) represent multi-way speciation events. They conclude that, without modification, the Felsenstein method can be used only with continuous characters, as discrete states cannot be applied to the Brownian motion model of evolution. When continuous characters are compared, the contrasts start at the tip of the phylogenetic tree, to contrast sister-taxa down to the root, which represents the common ancestor (Harvey and Pagel, 1991). The polytomies are split into two sub-nodes based on the value of each tree tip and the values for the node, estimated from the sub-node values (Purvis and Rambaut, 1995). Due to the assumption of Felsenstein's random walk process of evolution when continuous characters are used, many variables should be used in the form of a logarithmic transformation (Harvey and Pagel, 1991). When the test variable is categorical the nodal value of the character is assumed to be the same in all of the tips, or a contrast is computed amongst the tips. The only assumption made about the evolution of categorical traits by the programme CAIC is that of parsimony, assuming that when sister-taxa display a character state, the ancestor has the same state. CAIC has been used recently in many comparative analyses and seems to be very effective (e.g., Barton, 1996).

To make comparisons between two discrete characters, another comparative method must be employed. To account for the problem of non-independence, Ridley (1983) suggested that counting the changes in character states in different branches of the tree

could avoid the problem. He stated that the fundamental units in comparative analysis are the evolutionary events or transitions of a character. To perform the Ridley method, a phylogenetic tree is constructed using parsimony to reconstruct the ancestral state of the character. The number of transitions are counted along a branch (a transition is the change of state in either or both characters along the branch). Branches where there is no change are not counted, to avoid counting species that share a character state with an immediate common ancestor. This results in a two-by-two contingency table, similar to that used in the test of independence. The association of transitions between two characters are tested using a chi-square statistical test.

Maddison (1990) described a test to not only detect the pattern of evolutionary change as in Ridley (1983), but also the direction, by determining correlations of a character in different areas of the tree. The concentration of one discrete form would occur if the evolution of that form were more likely. Instead of both forms of the character being considered to be independent as in Ridley (1983), one is treated as the independent or causal variable and the other as the dependent variable. This test also involves all of the branches of the tree, whereas Ridley's method counts only the branches in which there is a change in character. Both tests assume that each relevant branch has an equal and independent probability of exhibiting the change in a particular character (Read and Nee, 1995). Neither test overcomes the major problem for comparative biologists of non-independence of data points. Read and Nee (1995) attempt to overcome this problem by devising the null hypothesis that a matched pair on either side of a node shares all of their characteristics until divergence. For each pair, the state of x is irrelevant to the state of y for a given character. If the states are different in x and y this has a probability of 0.5, therefore only variations in both x and y at a node affect the evaluation. The focus of this

test is on sister-taxa as it examines how *x* and *y* differ, not on the branches as a unit for comparison as described by Ridley (1983) and Maddison (1990). Also, as assumptions are only made about the changes in sister-taxa, they do not involve an evolutionary assumption, which makes this model different from those previously discussed.

1.9 Hypotheses

Predictions which have previously been proposed or suggested in relation to the evolution of primate colourations are listed in two parts. The first uses interspecific comparative tests to identify correlations with sexual dichromatism, pelage brightness and natal colouration. The hypotheses in 1.92 are derived from Hamilton and Zuk (1982). Table 1.1 summarises the origin of the predictions from functional hypotheses.

1.91 Interspecific correlations with primate pelage colour using comparative methods

A. Sexual dichromatism is associated with:

1. Polygamous mating (Andersson, 1994)
2. Sexual size dimorphism (Leutenegger and Chevereud, 1985)
3. Multi-male groups (Wickler, 1967)
4. Bright males (Darwin, 1871)
5. Bright females (Darwin, 1871)
6. Large group size
7. Natal colouration (Darwin, 1871)

B. Male pelage brightness is associated with:

1. Diurnality (Jacobs, 1981)
2. Sexual size dimorphism (Leutenegger and Chevereud, 1985)
3. Sexual dichromatism (Darwin, 1871)
4. Polygamy (Darwin, 1871)
5. Terrestriality
6. Female ornamentations
7. Multi-male groups (Andersson, 1994)
8. Brightly coloured genitalia (Darwin, 1871)
9. Male dominance (Wickler, 1967)

C. Female pelage brightness is associated with:

1. Diurnality (Jacobs, 1981)
2. No sexual size dimorphism or larger females
3. Female ornaments (Darwin, 1871)
4. Multi-male groups
5. Polygamy (Irwin, 1994)
6. Terrestriality
7. Large groups
8. Male dominance

D. Natal colouration is associated with:

1. Sexual size dimorphism
2. Multi-male groups (McKenna, 1981; Paul *et al.*, 1996; Treves, 1997)
3. Single-male groups (Treves, 1997)
4. Bright females (Darwin, 1871)
5. Bright males (Darwin, 1871)
6. Large group size (Alley, 1980; Treves, 1997)
7. Sexual dichromatism (Darwin, 1871)

1.92 Testing Intraspecific variation

Assumptions:

1. Parasite susceptibility varies between individuals and between species
2. Parasite susceptibility varies more between individuals in species displaying sexual dichromatism, or parasite load of the dichromatic species is greater
3. An individual's parasite susceptibility corresponds to the parasite load
4. Females choose the brightest males as mates
5. The relationship between parasite and host brightness is similar in all types of animal and are not specific to birds

Hypotheses tested:

1. Pelage reflectance varies between individuals but is greater between species
2. Pelage reflectance varies between sexes only in dichromatic species
3. Parasite load is negatively associated with overall pelage reflectance
4. Parasite load is negatively associated with the reflectance of specific morphological regions
5. Sexually dichromatic species are susceptible to a greater number of parasites
6. Parasites found in free-ranging animals do not differ from wild animals, but do differ from captive-bred animals

Hypothesis	Predictions	Variables
Evolution of sexual dichromatism is associated with sexual selection	Sexual dichromatism is associated with:	polygamy sexual size dimorphism male dominance multi-male grouping single male grouping group size bright males bright females
Evolution of a bright pelage is associated with sexual selection	Male/female pelage brightness associated with:	group size sexual size dimorphism polygamy multi-male grouping bright genitalia male dominance
Evolution of a bright pelage is associated with visual system	Diurnality is associated with:	bright males bright females
	Bright males and females are associated with:	natal colouration
Evolution of a bright pelage is associated with habitat	Bright males and females are associated with:	terrestriality
	Sexual dichromatism is associated with:	terrestriality
	Natal colouration is associated with:	terrestriality
Evolution of a bright pelage is associated with ornamentations	Bright males and females are associated with:	female ornamentation
Evolution of natal colouration is associated with sexual selection	Natal colouration is associated with:	sexual size dimorphism polygamy group size sexual dichromatism
Evolution of natal colouration is associated with infant defence	Natal colouration is associated with:	single male grouping
Evolution of natal colouration is associated with the paternity	Natal colouration is associated with:	multi- male grouping

Table 1.1: Summary of the functional hypotheses and their predictions to be tested

Chapter Two

Methods and Analysis (part one)

2.1 Variables used in the comparative analyses

Eight forms of ecological and behavioural variables were collected from the literature for 167 primate species to be analysed using comparative tests. Each variable is either continuous or categorical, depending on the nature of the variant.

Variable	Type
Activity	Categorical (Nocturnal/Diurnal)
Average group size	Continuous (No. of adults)
Mating system	Categorical (Monogamous/Polygamous)
Male dominance	Categorical (Dominant/Not dominant)
Male grouping	Categorical (Multi/Single)
Size dimorphism	Categorical (Present/Absent)
Female weight relative to male weight	Continuous (%)
Habitat	Categorical (Arboreal/Terrestrial)

Literature sources for data (in order of usage): Napier, 1976; 1981; 1985; Jenkins, 1989; Napier and Napier, 1967; 1985; Smuts *et al.*, 1987; Hill, 1965; 1966; 1972; Hrdy, 1977; Chance and Jolly, 1970; Clutton-Brock and Harvey, 1977; Erwin and Swindler, 1986; Fleagle, 1988; Jolly, 1985; Kavanagh, 1983; Schultz, 1969; Tattersall, 1982; Dunbar, 1988; Roonwall and Mohnhot, 1977; Richard, 1985, Ankel-Simons, 1983.

Table 2.1: Ecological and behavioural data

Variable			Type
Sexual dichromatism			Categorical
Natal colouration			Categorical
Female ornamentation			Categorical
Brightly coloured genitalia			Categorical
Male			
Female	}brightness		Continuous (1-3 scale)
Natal			
			crown
			cheek (not for natal)
Male			chest
Female	}reflectance	Continuous}	back
Natal			outer leg
			rump
			total

Sources: Reflectance measurements were made at the Natural History Museum, London and through field work at Duke University Primate Center, North Carolina, U. S. Brightness measurements were assessed through observation of animals at London and Edinburgh zoos.

Literature sources for colouration data and to supplement brightness observations (in order of usage): Napier, 1976; 1981; 1985; Jenkins, 1989; Napier and Napier, 1967; 1985; Hill, 1965; 1966; 1972; Hrdy, 1977; Jolly, 1985; Kavanagh, 1983; Schultz, 1969; Tattersall, 1982; Mitchell, 1979; Napier, 1970; Poirier, 1970; Smuts, 1989; Altmann, 1980; Fox and Vevers, 1960; Rowell, 1972; Wolfe and Sleeper, 1997.

Table 2.2: Colouration data

2.11 Sexual dichromatism

Presence of sexual dichromatism was only recorded when there was an overall difference in pelage colouration between the sexes. It was not possible to treat sexual dichromatism as a continuous variable by quantifying the pelage variation by grades, due to the problems of categorising slight colour variation on a continuous scale. Only the presence/absence of sexual dichromatism was used in the comparative analyses, species possessing sexually dichromatic pelages were categorised as 1 and other species 0.

2.12 Female ornamentation and bright genitalia

Minor colour variations or coloured ornamentations such as a mane or whiskers in only one sex were not considered to be pelage sexual dichromatism. In some cases, noted in Appendix 1.7, only the female displays some form of ornamentation (colour and/or hair tufts or whiskers). In other species, the ornamentation or colouration of the genitalia differs. Tests were performed to compare female ornamentation and bright genitalia with ecological and colouration correlates. Species were deemed as displaying female ornamentation when there was some colour variation in the adult females that was not present in the males. Species categorised as possessing bright genitalia displayed rump, penile or scrotal colouration with hair or skin that was different to that of the pelage (see Appendix 1.6). It must be noted that species that display oestral reddening of the skin were not included, as the colouration must be a permanent feature, and not related to sexual seasons. Each species

was classed on possession of the feature: present = 1, absent = 0. Comparisons using these two categories were limited, as both forms are categorical and could therefore only be compared with variables, which were classed as continuous, such as group size or body weight.

2.13 Natal colouration

Some species have infants that differ in minor features from the adult pelage, such as a coloured brow band or a hair parting showing scalp colour (Alley, 1980). These species were categorised 0, as were species where there was no evidence of a natal coat. Only when the infants were more than 50% different from both parents was a species considered to display natal colouration and categorised as 1. Natal colouration could not be treated as a continuous variable as the categories did not equate with measurements. It was decided that the dichotomous presence of assessing natal pelage variation was a more concise and accurate method of assessing pelage colour variation.

2.2 Primate vision and the assessment of pelage brightness

The visual impact of the brightness of an individual is difficult to quantify, as it depends not only on the colour of the pelage, but the patterning and distribution of colour in the form of stripes, spots, etc. Hair and skin colours although constrained by the chemical limitations of

pigments and capillary blood flow, can differ dramatically between individuals. Ornamentations also contribute to the brightness of an individual, which was accounted for when assessing species brightness and was considered separately (see Appendices 1.6, 1.7).

The first method used to quantify overall pelage brightness was the standard assessment of visual brightness, using a scale to quantify colouration. This method is a commonly used method of assessment in brightness and colouration studies. In this study pelage brightness was assessed using all possible safeguards which were outlined by Endler (1994), to objectively assess the nature of a primate pelage. The term 'brightness' is "the summed contribution from different cone types" (Endler, 1994, p. 849). Therefore the quality of the visual assessment of brightness is dependent on the observer's assessment of a bright colour. In an ideal situation an objective, independent observer would have been used to attribute brightness values to the species from photographs. Unfortunately, due to the nature of the data collection (from zoo visits, photographs and descriptions from the literature) this method was impossible. Controversy has also arisen in using the method of visually quantifying the brightness of taxa with different visual systems (Endler, 1994). In species such as birds and fish, the visual system is so different from our own that the brightness perceived by the animals themselves corresponds little to humans (due to the wide variation in cone types). Endler suggests minimising this problem by using the natural receivers to assess colour differences (Endler, 1994). The justification for the use of the observational assessment of brightness in this study is the similarity between the perceived colours of vision in humans and diurnal primates, in particular the anthropoids. The visual system differs among primates: Catarrhines have trichromatic vision (Old World monkeys are

functionally monochromatic), platyrrhines exhibit either trichromatic or dichromatic vision, and the diurnal lemurs, indrii, sifaka and tarsiers exhibit dichromatic vision. The remaining strepsirhines all are nocturnal with monochromatic vision (Jacobs, 1981). Dichromatic vision allows two wavelengths of colour to be visualised by two types of cone, short wavelength sensitive (S), in the blue part of the spectrum and long wavelength sensitive (L), in the red part of the spectrum (Jacobs, 1993). Trichromatic species have a third, medium wavelength cone (M), in the green part of the spectrum. Most mammals have dichromatic vision and it has been suggested that trichromatic vision in primates is an adaptation to frugivory, useful in identifying food sources (e.g., Jacobs, 1981; Osorio and Vorobyev, 1996). Birds are natural tetrachromats, possessing at least four cones (Chen *et al*, 1984), and therefore the method of visual assessment by humans would be a more inappropriate method to use than humans assessing the colours of other primate pelages. Indeed "the inability of humans to perceive the colour world of animals applies most dramatically to the birds" (Endler, 1994, p. 852).

Pelage brightness was assessed as the overall visual effect of the pelage colour including the colours of body parts, although these were not considered separately. As when assessing the natal colouration and sexual dichromatism of a species, the brightness of a pelage was also considered in the context of where it would be seen. Therefore the location of the species and it's lifestyle in terms of arboreality or terrestriality, and general habitat colour were also considered when attributing a value to the brightness of a species. When there were differences between age and sex in pelage colouration, the assessment was divided into the

appropriate categories to quantify the brightness of a species based on the observations of several individuals in the same category. The error of assessment using a brightness scale of 1-3 and category boundaries, was reduced by examination of pelage colourations of primate species at London and Edinburgh Zoo and from viewing skins at the Natural History Museum, London.

The ranked scale is 1-3,

1 = a visually dull pelage such as agouti (common in nocturnal primates).

2 = of average brightness, some colour variation, few or no bright colours or patterning.

3 = Brighter than average, displaying vivid colours or highly contrasting patterns.

When quantifying pelage colour brightness, the visual impact must also depend on the surrounding habitat. For example, when considering natal colouration the orange colouration of the infant langur, *Presbytis cristata,* is considered to be very bright due to the nature of the colour alone, despite the pelage being monochromatic with no patterning. When the infant pelage is considered in an arboreal habitat (primarily green), where the species would commonly be found, the colour also appears very bright. Yet, the same infant placed in a savannah habitat would have less visual impact, as the orange colour would not contrast with orange/yellow surroundings. Therefore, the adult pelage and species habitat were also considered in addition to the nature of the pelage itself, when visually assessing the brightness of a pelage. Due to the outlined problems of assessing pelage brightness two methods were used, a visual assessment using a ranked scale and a measured assessment of reflectance using a continuous scale.

2.21 Measuring reflectance

A more accurate method of assessing the nature of a pelage colour requires making direct measurements, which can be done using reflectance. Measuring colouration on a continuous scale also enables identification and quantification of small brightness differences between individuals. There is no specific equipment designed to measure pelage brightness, which is why the visual assessment of brightness is commonly used. However, a reflectance spectrophotometer is used to determine variations in human skin pigmentation. In this study, it was used to measure the reflectance of pelage colours. The spectrophotometer was used in both parts of the research, in testing inter-and intraspecific correlations.

The reflectance of colour is the physical component of a colour which is not altered by the receiver, and is not therefore dependent on the receiver's ability to perceive a range of wavelengths, dependent on the possession of various cones. Therefore, the reflectance spectra of a pelage colouration can be quantified independently of the observer, whereas the brightness cannot (Endler, 1994). Pelage brightness measurements correspond to the reflectance; white fur gives a high reflectance reading of 60-100%, and black fur has a reflectance of 1-5%. Figure 4.1 illustrates how pelage colouration corresponded to reflectance measurements. Some colours that visually appeared bright, such as reds and oranges, gave very low reflectance measurements. This finding illustrates that the brightness of colours, as visually perceived, may not correspond with a highly reflectant reading. This would be expected as Endler described colour as "a product of the brain of the animal perceiving the object, and not an inherent property of the object" (Endler, 1994, p. 856. For

this reason, the visual scale was considered to be a more useful method for quantifying brightness differences between species for comparative analysis. Whereas, the spectrophotometer measurements were useful to identify differences in brightness between individuals of the same colour, hence, it was a more appropriate method of measuring intraspecific colour variations enabling predictions made by Hamilton and Zuk (1982) to be tested. Use of the spectrophotometer in testing intraspecific hypotheses was a much better method of identifying individual brightness variations, because we assume that intraspecific variation related to the health of individuals is revealed by glossiness and reflectance rather than by wavelength.

2.22 The 'Eel' reflectance spectrophotometer

The equipment consists of a light source head and a Galvanometer unit. The reflectance spectrophotometer head (Fig. 2.1) has a 6 watt, 6 volt lamp with a ventilated holder and a heat absorbing glass filter, preventing heat transfer to the photocell through which light is directed at the bottom of the head. Light is reflected from the pelage onto the photocell generating a current that is transferred to the galvanometer unit. The spectrophotometer head has a selection of four filters specific to requirements. The 605nm filter was selected for measuring brightness. This was the most appropriate filter, as it corresponds to the yellow green colour, midway between the visible spectrum enabling accurate measurements of wavelengths from 600nm, deep violet to 609nm, deep red (Fig. 2.2). The galvanometer has a scale of 0-100, which corresponds to percentage reflectance. To enable accurate

measurement of the reflectance of colour, a standard absolute white source of magnesium carbonate is used to calibrate the galvanometer scale to measure 100% reflectance. This is the reference point for all brightness measurements and is calibrated after each measurement.

2.23 Measuring the brightness of individuals

Representative adult males, females and natals were selected for quantification of species brightness. All reflectance measurements were made using primate skins (47 species) at the Natural History Museum, London. To assess the total pelage brightness of an individual, six body parts displaying the most sex- and age-related colour variations were measured (see Appendix 1.12). These were the crown of the head, cheek, upper back, chest, outer upper thigh and the rump. The cheek area was not measured for brightness in infants or very small primates, such as the dwarf lemur (*Cheirogaleus medius*) as the area was too small to be accurately measured. Ornamentations and extra features, such as sexual skins, were not measured, as only sexual dichromatism was to be considered in this study, not small sexual differences. Two values were measured for each body part to calculate the individual average reflectance. For three species, there were a number of available skins. Repeat measurements were made on five different skins to calculate the pelage brightness variation between similar members of the same species. Multiple skins were only available for adult males (see Appendix 1.11). The standard deviation was calculated for the intraspecific variation for the three species and compared to the interspecific standard deviation between the three species. The two results were compared to identify if interspecific variation was

greater than the intraspecific variation in pelage reflectance. Concerns in using the pelage reflectance measurements of dead animals, (some for over 100 years!) which may have dulled the colours or have a lower reflectance, due to ageing and preservation methods used on the skins were tested using a paired t-test. The reflectance measurements of live *Lemur catta* (n = 10) used in the second part of this research were compared with the reflectance measurements of the dead museum specimens of *Lemur catta* (n = 2) in the form of a paired t-test.

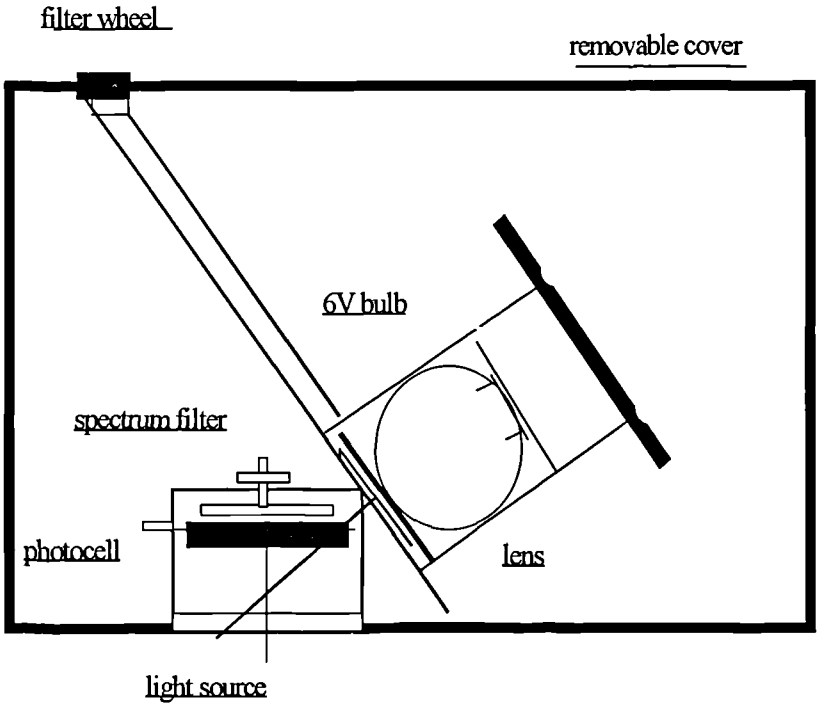


Figure 2.1: Reflectance spectrophotometer head

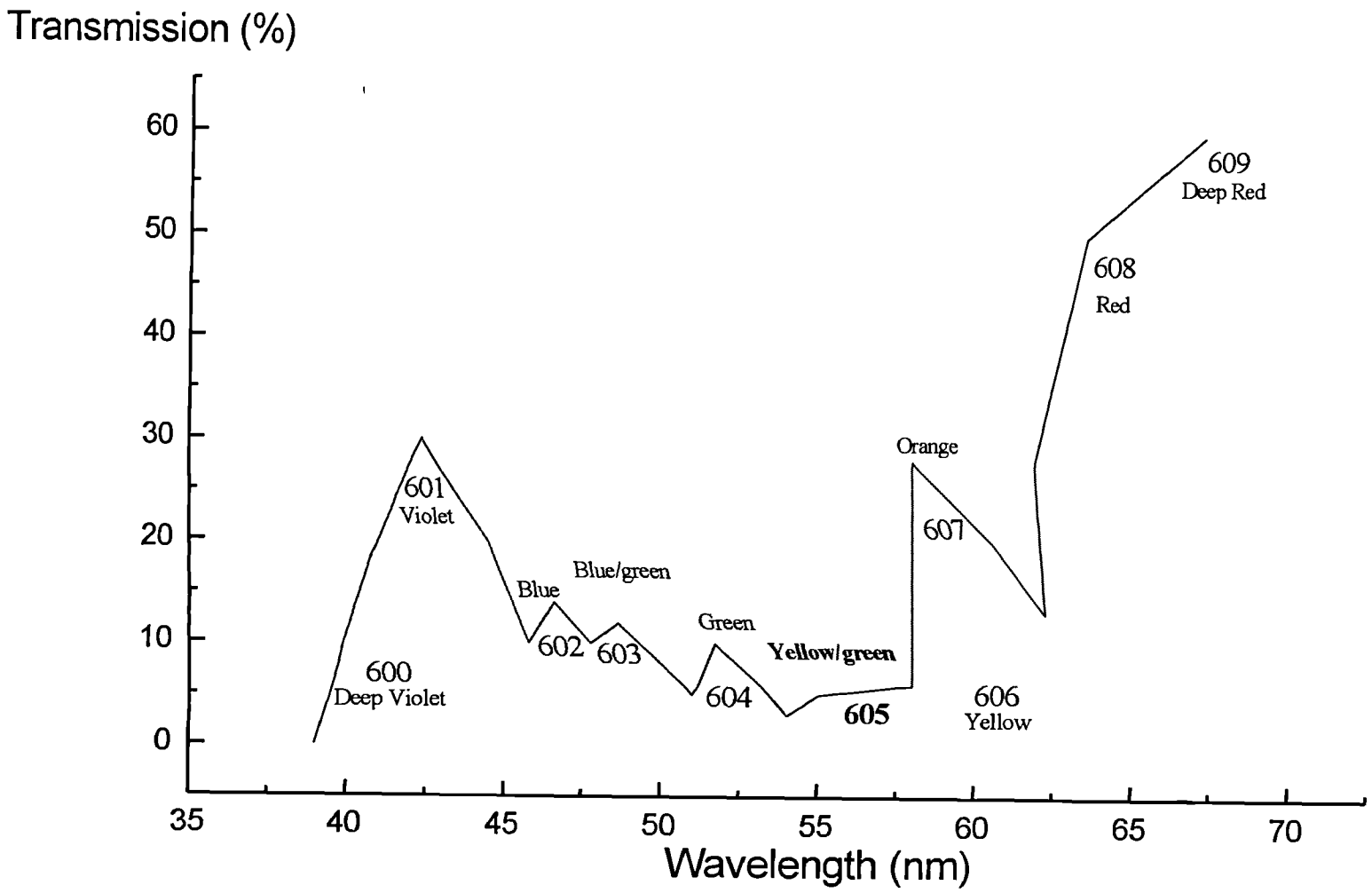


Fig. 2.2: Spectral transmission for the 'Eel' reflectance spectrophotometer

2.3 Mating system, group size and dominance

Species that display multi-male grouping were categorised as a 1, single male grouped species were categorised as 0. Species for which there was some conflict over the practice of monogamy or polygamy were excluded from the analysis (e.g., callitrichids). Polygamous species were categorised as 1, and monogamous as 0. The average group size of a species was obtained directly from the literature, when more than one size was given or there was a range of numbers of individuals in a group, the mean number of individuals was recorded. Male dominant species were categorised as 1, and female dominant as 0.

2.31 Body weight and sexual size dimorphism

Sexual size dimorphism was assessed using two forms of measurements to ascertain if a species was sexually size dimorphic. Body weights were given for both sexes (e.g., Table 16-1 in Smuts (1987) of body weights taken from wild or captive animals), or the percentage difference in body size was quoted as female weight as a percentage of male weight. The body weights that were collected from the literature were described as a percentage of male body weight to account for comparisons of sexual size dimorphism in a species. If a range of weights were given for a species then the median was calculated. For species in which both male and female body weights were obtainable, the female weights were calculated as a percentage of male body weight (see Appendices 1.2-1.5). Females that were less than 90% the body weight of the male in the same species were classed as sexually

size dimorphic and awarded category 1 to describe the presence of sexual size dimorphism. Species with female body weights greater than 90% of male body weight were not considered to be size dimorphic and categorised as 0. This binary method of categorising presence of sexual dimorphism was used in the initial stage of the research where the distribution of size dimorphism across the order was examined. The binary method was also used to categorise size dimorphism when performing further comparative analyses, but only after comparisons gave a significant result using the quantitative index of dimorphism. Where accurate weights were provided for both sexes, the mean weight of each sex was also included in the analysis to serve two purposes. Firstly, to compare the 90% male body weight threshold with continuous weights to include smaller weight differences between the sexes, and secondly, to determine if by using continuous variables instead of dichotomous variables, there would be a different outcome after phylogenetic adjustment.

2.32 Habitat

There are four main categories of habitat inhabited by primates as described by Clarke (Richard, 1985): tropical rain forest, savannah, steppe (transition between savannah and desert) and desert. The species may be arboreal or terrestrial; usually arboreal species are found in rain forest and savannah habitats, and terrestrial species in savannah, steppe and desert habitats. For the purpose of analysis using CAIC, the habitat description grouped all primate species into two broad categories; arboreal and terrestrial. This was because comparisons made in CAIC can only be made between a binary categorical variable and a

continuous variable, or two continuous variables. This would have reduced the number of hypotheses that could be tested. In reality, primates inhabit a wide range of habitats with many species living in more than one defined habitat type. For example, *Lemur catta* (ring-tailed lemur) spends the majority of its time foraging and playing on the ground, but sleeps in the tree canopy (Tattersall, 1982). The category of arboreality or terrestriality was assessed from literature sources, dependent on the time a species spends locomoting, feeding and sleeping on the ground or in the trees. Considering *L. catta* as an example, most of the activity time is spent on the ground, therefore it should be categorised as a terrestrial species. All information concerning habitat was obtained from Smuts *et al.* (1987), Napier (1976, 1981, 1985) and Jenkins (1989). Arboreal species were categorised as a 0, and terrestrial species were categorised as 1.

2.33 Categorising the activity pattern of a species

Species were only classified as diurnal or nocturnal. Those displaying crepuscular activity were classified dependent on their retinal structure (i.e., the retinal structure of some lemur species that are described as crepuscular were classed as diurnal). The retinal structure, however, did not define the activity of the species in question, as ultimately the behaviour of the species was of importance; therefore, the owl monkey was categorised as nocturnal despite possessing a duplex retina. Diurnal species were categorised as 1, and nocturnal species as 0.

2.34 Species taxonomy and phylogeny

The phylogeny constructed by Purvis (1995) has been used to name all primate species in this study and the cladogram has been used when performing comparative analysis using CAIC and the binary method. The phylogeny is composed of 203 species, but only 163 species were included in this study due to source availability for newly named species and the less studied or rare taxa. There are often discrepancies between classifications of a species or a sub-species. For example, tarsiers, *Tarsius pumilus* and *Tarsius dianae,* have now been given individual species status (Niemitz, 1994). Taxa that have been recently awarded species status have not been included in this research as the data set was constructed between 1994-1997.

2.4 Comparative tests

There are four parts to the analysis of the large dataset (given in Appendices 1.3-1.5). The first examines how sexual dichromatism and natal colouration are distributed throughout the order Primates. The first comparison tests seven specific hypotheses associating the presence of sexual dichromatism and natal colouration with mating system, and sexual size dimorphism using the test of independence (*G*-statistic). Sokal & Rohlf (1981) describe the test of independence using contingency tables as the most appropriate statistical test of whether two different properties, occurring in two states, are dependent on each other. There are three kinds of tests for independence that use 2 x 2 tables: *G*-test, Fisher's exact test, and the chi-square test (Sokal & Rohlf, 1981). Each test is designed for a specific model. The *G*-test is designed for model I, in which the sample size *n* is the same for both properties.

The second set of analyses uses CAIC (Purvis and Rambaut, 1995). A large dataset was used to test a list of hypotheses involved with sexual dichromatism and pelage brightness (see section, 1.3 A, B and C). CAIC is designed to account for the non-independence of species data points, which can create false patterns and miss real patterns when making comparisons across species, as the closer relatives are more similar, sharing more characteristics than would be expected by chance. CAIC uses Felsenstein's principles of phylogenetically independent comparisons with modifications as recommended by Burt (1989), Pagel (1982), and Purvis and Rambaut (1995). The final analysis uses the Binary

method developed from Ridley by Read and Nee (1995).

The three analyses, tests of independence, CAIC, and the binary method, were also used to test hypotheses associated with the evolution of natal colouration in a species. The same procedure was used as will be described below and the same datasets (See Appendix 1.2-1.5). The hypotheses do differ from those used in the analyses with sexual dichromatism and are listed in the Introduction 1.3 (D).

A second part to the study involves the examination of pelage variation between two lemur species. A comparative analysis was used to test predictions made by the Hamilton-Zuk hypothesis (Hamilton and Zuk, 1982). CAIC was used to compare correlations as both inter- and intraspecific analyses were required to test the hypotheses (see section 1.32). The procedure of performing the analyses will now be described.

2.5 Distribution of colouration states: sexual dichromatism and natal colouration

The first stage of the study was to quantify the number of primates that display intraspecific colour variation in the forms of sexual dichromatism and natal colouration. One hundred and fifty six species were divided taxonomically into the suborders Strepsirhini and Haplorhini, the latter containing the infraorders Tarsoidea and Anthropoidea (Platyrrhini and Catarrhini). Species were categorised as nocturnal or diurnal and the distribution of sexual dichromatism and natal colouration was recorded as a percentage and as number of species.

2.6 Two-way table comparisons and the test of independence

The analysis uses a two-way analysis of the test of independence as described in Sokal and Rohlf, (1981). Each hypothesis is constructed using two variables to be compared, appropriate to the hypothesis. This method of comparison did not account for the evolution of similar characters between closely related species, and was expected to give different results to the subsequent tests that account for interspecific comparisons. The initial comparisons have been performed to illustrate how the results can be biased, given the number of characteristics that are shared between closely related species. Analysis of the data was performed twice, initially including nocturnal species in the analyses. The result of including nocturnal species in the first set of tests should alter the result, as the object of interest in the analysis was colouration variation. Colouration should not exert a selective evolutionary effect on nocturnal species as the majority of nocturnal species have monochromatic vision. This is further illustrated by the lack of intraspecific colour variation in the nocturnal primates. All seven comparisons were repeated, excluding nocturnal species, the implications of which will be discussed in the following chapters.

Each two-way table was used to test one of five hypotheses:

1. Sexual dichromatism is associated with natal colouration.
2. Sexual dichromatism is associated with sexual size dimorphism.
3. Sexual dichromatism is associated with mating system (multi- or single male).
4. Natal colouration is associated with sexual size dimorphism.
5. Natal colouration is associated with mating system (multi- or single male).

The data are displayed as a count for the number of species observed. The first hypotheses were tested as two-way tables with and then without nocturnal species, of which there were 26. In total, the test of independence was performed using 14 two-way tables of varying combinations of the ecological and morphological features with reference to the hypotheses (see Appendix 2.1). Below is an example of how a two-way table using the *G*-statistic was used to identify correlations between two variants.

Example 1. Two-way table showing species data from hypothesis 1. (26 nocturnal species omitted).

Hypothesis 1. Sexual dichromatism is associated with natal colouration in primates

no. species		Sexual dichromatism			Total
Natal colouration		presence		absence	S
presence	a	10	b	38	$a + b$ 48
absence	c	8	d	74	$c + d$ 82
Totals	$a + c$	18	$b + d$	112	n = 130

The observed frequencies were used to perform the test of independence using the *G*-statistic with the Williams correction; the correction is required for data using a 2 x 2 table (Sokal & Rohlf, 1981). The formulae shown uses the data from Example 1:

1. $Sf \ln f$ for the cell frequencies.

$$= 10 \ln 10 + 38 \ln 38 + 8 \ln 8 + 74 \ln 74$$
$$= 496.39$$

2. $Sf \ln f$ for the row and column totals.

$$= 48 \ln 48 + 82 \ln 82 + 18 \ln 18 + 112 \ln 112$$
$$= 1127.68$$

3. $n \ln n = 130 \ln 130 = 632.77$

4. Compute G using expression : $G = 2$[quantity 1- quantity 2 + quantity 3]

$$= 2[496.39 - 1127.68 + 632.77]$$
$$= 2[1.48] = 2.96$$

5. Williams' correction for a 2 x 2 table is

$$q = 1 + \frac{\frac{n}{a+b} + \frac{n}{c+d} - 1 \frac{n}{a+c} + \frac{n}{b+d} - 1}{6n}$$

For the previous data :

$$q = 1 + \frac{\frac{130}{48} + \frac{130}{82} - 1 \frac{130}{18} + \frac{130}{112} - 1}{6(130)}$$

$$= 1.03$$

G adj $= G/q = 2.96/1.03 = 2.87$

6. G adj, the adjusted G statistic is compared with the critical value of χ^2 for one degree of freedom. If G adj is less than $\chi^2_{0.5[1]} = 3.841$, then the null hypothesis of independence is accepted (Sokal & Rohlf, 1981).

In the above example, G adj $< \chi^2_{.05[1]}$. Therefore, the null hypothesis that the evolution of sexual dichromatism is independent of natal colouration is accepted. Further tests of independence were performed to determine the association between the mentioned features for all species. Where mating system was compared with sexual dichromatism or natal colouration, either single male or multi-male grouped species were compared against single male or multi-male species and other grouped species such as monogamous family groups. The initial set of seven tests included the nocturnal species and the second set excluded the 26 nocturnal species. Fourteen two-way tests of independence were performed (see Appendix 2.1).

2.7 Comparative Analysis by Independent Contrasts (CAIC)

The next stage of analysis using the comparative method was to test a larger range of hypotheses for the diurnal primates accounting for phylogenetic non-independence. The database was compiled from the variables discussed in Chapters 1 and 2, and the colour

variation of each species was defined using the methods described (see Appendices 1.2-1.5). Data were sorted into columns for entry into the program CAIC (Purvis & Rambaut, 1995) as previously discussed and defined as either categorical or continuous variables. The phylogeny for the order Primates (Purvis, 1995) was entered into the program for analysis and 163 species in the database were matched with the phylogeny. Five species could not be matched, which can be attributed to the rapid turnover of the naming of primate species and sub-species. These species could not be included in the comparative analysis and therefore the total number of species analysed was 158. Columns were analysed in pairs appropriate to the hypotheses for example, sexual dichromatism is correlated with group size.

One variable was selected as the "predictor" or independent variable, which was sexual dichromatism for the example above. Each output of standardised linear contrasts was saved in individual files for further statistical analysis. All appropriate contrasts were made according to the hypotheses listed in the introduction. Comparative analyses were first performed including nocturnal species. The analysis was repeated after omitting the nocturnal species from the dataset, therefore removing any swamping effects attributable to this ecological variable. Colouration data were compared with other variables, using the 1-3 visual scale of pelage brightness and the reflectance measurements. All initial comparisons tested the overall brightness; then significant cases were broken down by body part. The mean pelage reflectance was included for two comparative tests where the reflectance of three body parts or more were significantly correlated with sexual size dimorphism.

The output from CAIC was analysed by one of two ways depending on the form of data in

the columns. When both variables were continuous, the "Crunch" algorithm was used. In this case, one of the variables is assigned as the predictor variable, which will be positive, or zero, if there is no variation for the assigned character between the variables. The results for the variables being compared with the predictor variable can be either positive or negative, depending on how the variables follow or contrast with the predictor variable for that characteristic. Outputs from using the "Crunch" method are statistically analysed using regression analysis (see Appendices 2.3, 2.4). The algorithm "Brunch" is used when one of the variables defining a characteristic is categorical, categorised as present or not using a binary code of 1 or 0. Outputs from using the "Brunch" method in CAIC are analysed using a one-sample tailed *t*-test with a hypothesised mean = 0 (see Appendix 2.2). The results of performing a "Brunch" contrast can be positive or negative. A positive contrast indicates that the variables are varying for that characteristic in the same direction, (i.e., higher values for the category are assigned as "1"). A negative contrast indicates the categorical and continuous variables are varying in "opposite" directions. Tests were performed using either the Crunch or Brunch algorithm (see Appendices 2.2-2.4). There were limitations of using the program, as it was not designed to make comparisons between two categorical characteristics. Several categorical (dichotomous) comparisons were necessary to answer several of the hypotheses. Therefore, another method of making comparisons was required which would also take account of any phylogenetic similarities for the characteristics. This was the binary method of Read and Nee (1995).

All output files from the program CAIC were analysed in the Macintosh version of Statview 4. Output files saved from a Crunch comparison, where all variables were continuous (such

as body weights or brightness measurements), were analysed using a linear regression. The bivariate hypothesis, as described by Harvey and Pagel (1991), determines if X and Y are correlated; X is the predictor variable and Y is the dependent variable. When the regression is forced through the origin, the value of the slope shows the relationship between the variables X and Y. The spread of the plot and any outlying points were noted. The p and t values and the degrees of freedom were calculated for every output file from a comparison. Scatterplots were inspected for outliers. In one comparison, there was an extreme outlying point, which was removed. The number of species was also recorded for each comparison, as it varied depending on the data available for each characteristic.

The output files from Brunch comparisons, where one of the variables was categorical (e.g., presence of sexual dichromatism), were analysed using two-tailed t-tests. According to the null hypothesis, that the evolution of the characteristic of the continuous variable (the dependent variable) is not associated with the evolution of the categorical characteristic, half the contrasts for the continuous variable should be positive and half negative (Purvis and Rambaut, 1995). A bias towards positive scores indicates that the evolution of X with respect to Y correlates a high value of X characteristic with a large Y (where X was coded as 1/0). Conversely, a negative result indicates that a high value of X correlates with a small value of Y. Scores recorded from the t-test were the same as for the regressions; p-values, t-values, the degrees of freedom and the number of species in the comparison. All p-values were considered to be significant at $p \leq 0.05$, and $p \leq 0.1$ were reported.

Multiple regressions were performed to test if some variables were confounded with each

other, as suggested by Purvis and Rambaut (1995). This method identifies if the variables which are considered to be "independent" are in fact having an confounding influence over the significance of the comparisons. A multiple regression was performed on the variables of average group size, sexual size dimorphism and pelage brightness. Three multiple regressions were required to include male, female and natal pelage brightness where each was assigned as the dependent variable Y. Average group size and degree of sexual size dimorphism were assigned as the independent variables X.

Several additional comparisons were performed using the same methods of CAIC and statistical analysis, but that did not include any form of colouration variable. These were used to identify if indeed any variables were associated and not independent of each other, as assumed in the analysis.

2.8 The binary method of analysing comparative data

Comparisons by independent contrasts are limited to those between continuous and categorical variables or between continuous variables alone. An alternative method was required to test hypotheses where there were comparisons between two categorical variables; for example, sexual dichromatism is associated with sexual size dimorphism,

where both sexual dichromatism and size dimorphism were categorised as present or absent (1/0), (although size dimorphism was also measured on a continuous scale as % male body

weight). It was necessary to test for associations between natal colouration and sexual dichromatism with five other categorical variables: multi-male/single male grouping, monogamous/polygamous, arboreal/terrestrial, size dimorphic/not, male dominant/not (as discussed in the introduction). An alternative method of comparing binary comparative data, and still account for evolutionary relationships between closely related taxa was designed by Read and Nee (1995), following Ridley (1983). This method uses a model of randomness through the random assignment of treatments, which they argue provides a rational acceptable basis for inference. The model assumes that states are assigned randomly between sister taxa that display varying states of a variable. This allows the probabilities of the evolution of a character to vary throughout the phylogeny without assumptions being made as to how the evolution occurs.

To perform the appropriate tests using the Binary method, a valid phylogeny is required. For this purpose the phylogeny used in the CAIC comparisons was used (Purvis, 1995). All comparisons had to be tested manually as a computer programme has not yet been designed for this method of comparison. For example, the presence of dichromatism or dimorphism was drawn onto the cladogram from the tree tips corresponding to every species for which there was data available. Figures 4.4 - 4.8 show how the binary method was performed. The left-hand side shows part of the phylogenetic tree for the order Primates. Both sexual dichromatism and natal colouration have been drawn onto the tree to show the distribution and evolution of both characters. On the right-hand side of each figure is a table where the presence or absence of each variable was assigned as a 1 or 0, for each of the characteristics. Sexual dichromatism and natal colouration were compared separately against five variables.

From the cladogram, sister-taxa are defined for each variable, but each species can only be used once in the comparisons, as paths linking sister-taxa cannot cross. The number of contrasts at the tree tips for a characteristic *x*, and the frequency of occurrence with characteristic *y*, are counted at the nodes between sister taxa. A binomial distribution is used to describe the comparisons of characteristics. Presence of characteristic *x* with characteristic *y* is assigned number 1; if characteristic *y* is not present when *x* is present with a contrast in characteristic, the contrast is described as 0. A one-tailed binomial test was used to determine if the characteristics were occurring more frequently than would be expected by chance under the null hypothesis of random allocation of the state of *x* (Read and Nee, 1995). All of the comparative tests performed gave a small number of contrasts, the greatest number being ten. These small sample sizes are an unavoidable consequence of accepting the logic of the comparative method.

2.9 Comparative tests and false-positive results

Due to the number of comparative tests performed it would be expected that some of the significant results could have occurred by chance alone, highlighted by Bonferroni (Sokal and Rohlf, 1981). This type of error must be seriously considered when conducting a number of comparative tests. The number of tests performed in a sample should be limited as much as possible. This does not, however, stop errors of this form occuring. In this study, the number of significant results which could occur by chance alone were calculated for each comparative result table. At a significance level of 5%, 100/5 multiplied by n comparisons

gives an estimate of the expected number of significant results expected by chance alone. These were calculated for Tables 4.3 – 4.6 and also Tables 5.2 – 5.4.

Chapter 3

Methods (part two)

3.1 Testing the Hamilton-Zuk hypothesis in lemurs

The second part of this study is an intraspecific test of the Hamilton-Zuk hypothesis. It states that the potential quality of a mate is judged according to the presence of genes for parasite and pathogen resistance, made evident by a bright pelage colouration (Hamilton and Zuk, 1982). If an individual's susceptibility to parasitism is important in sexual selection, then it would be expected that species which show strongly developed epigamic characters, such as a bright pelage colouration, must be subject to a wider variety of parasites. Conversely, species in which parasitism is less prevalent should display fewer secondary sexual characters such as sexual dichromatism. Intraspecifically, variation in parasite resistance should be correlated with brightness. The main focus of the study was to identify and measure the variation in colouration between individuals within two lemur species, then to associate this variation with the parasite load of an individual, and finally, to compare the intraspecific variations between the two species, one of which is sexually dichromatic. The two lemur species *Eulemur fulvus rufus*, the red fronted lemur, and *Lemur catta*, the ring-tailed lemur, were selected because they live sympatrically and therefore share ecological characteristics associated with the habitat. Both species have a similar social system, both are diurnal, and both share the same diet. Therefore, it can be surmised that as both species share very similar characteristics, there must be some other variable that has not been identified which could contribute to the presence of sexual dichromatism in only one of the two species. This characteristic could be associated with parasitism and health.

Endo parasites are present in the host's body and measuring endoparasite load from

blood or faeces is common. As blood collection is an invasive technique which stresses the individual permission would not be granted to conduct this form of parasite load assessment on lemurs. However, faecal sampling is an effective non-invasive technique of assessing the endoparasite load of an individual and permission was allowed to conduct the study at Duke University Primate Center. Faecal samples were collected from the two lemur species and analysed to assess the parasite load of individuals. The load of each individual was then compared with the pelage variations that were assessed using a reflectance spectrophotometer. Faecal samples were also collected from two lemurs at London Zoo and from a number of *Lemur catta* individuals living wild in the forests of Madagascar. The following sections outline the methods used for this part of the study.

3.11 The Duke University Primate Center (DUPC)

Located in the forests at Durham, North Carolina in the USA, the Center specialises in the captive breeding and study of endangered strepsirhines: the lorises of Asia, the galagos of Africa, and the lemurs of Madagascar. Funding from the National Science Foundation (N. S. A.), Duke University and private donations enables captive breeding and the return of suitable animals to homeland reserves. The size of the colony is over 500 individuals representing 29 species and sub-species, including seven of the most severely threatened species. The Malagasy lemurs are now the most threatened group of primates World-wide. Some species are kept in an enclosed facility at the centre with six enclosures of varying shapes and sizes in the surrounding forest containing free-ranging troops in their natural environment. The six enclosures are divided by natural boundaries with an external electrified perimeter fence surrounding the site (Fig. 3.1).

The lemurs studied were present in two natural habitat enclosures with a stream providing a natural boundary between NHE-2 and NHE-4 of the free ranging captive lemur collection. Enclosures NHE-2 and NHE-4 both contain three species: *Lemur catta*, *Eulemur fulvus rufus* and *Varecia variegata variegata.* One troop of *Lemur catta* and *Eulemur fulvus rufus* were in each of the two enclosures and the *Varecia* troop ranged between both enclosures. Only *Lemur catta* and *Eulemur fulvus rufus* were used here.

3.12 Individual identification

Individuals of *Lemur catta* are very similar without sexual or ontogenetic colour variation (refer to Fig. 3.2). *L. catta* is predominantly grey with a brown tinge across the back. Ventrally they are white; this extends to the face which is mostly white centred by a black muzzle and small black orbital rings. The crown region is grey and the ears white. All limbs are grey with a brown tinge. The most striking feature of *L. catta* is the tail, which is vertically banded black and white with a white tip. The tail is used for signalling and marking and is carried erect when travelling on the ground. *Eulemur fulvus rufus* displays sexual dichromatism, but unusually it is the female that is more striking and bright in appearance (refer to Fig. 3.3). The female is predominantly a ginger/red with a slight grey tinge. The head and face are mostly white, with a grey patch on the crown separated by a brown stripe. The muzzle is black, as in the male and extends to the forehead and around the orbits. The ears are grey, and the limbs and tail a ginger/red, the same as the majority of the pelage. Males are predominantly grey with a face similar to the females, and the crown is the ginger/red of the female pelage. As females are brighter it is possible that reversed sexual dimorphism may be present in *Eulemur fulvus rufus,*

and therefore a negative correlation between brightness and parasite load could apply to the females instead of the duller males.

The two *Lemur catta* troops were larger (38 individuals in total) than the *Eulemur fulvus rufus* troops (15 individuals in total); therefore, faecal and brightness data collection concentrated on most individuals in the group NHE-4. Representative individuals of *E. f. rufus* were used from both enclosures. The fieldwork took four weeks to collect faecal samples, including two days of netting to make the brightness measurements and six months to complete the faecal analysis and assess parasite loads. Time was spent habituating with the lemur troops and following the troops to the feeding and resting sites. Individuals were relatively easy to identify through the colour and shape of collar and tag (Tables 3.1 and 3.2).

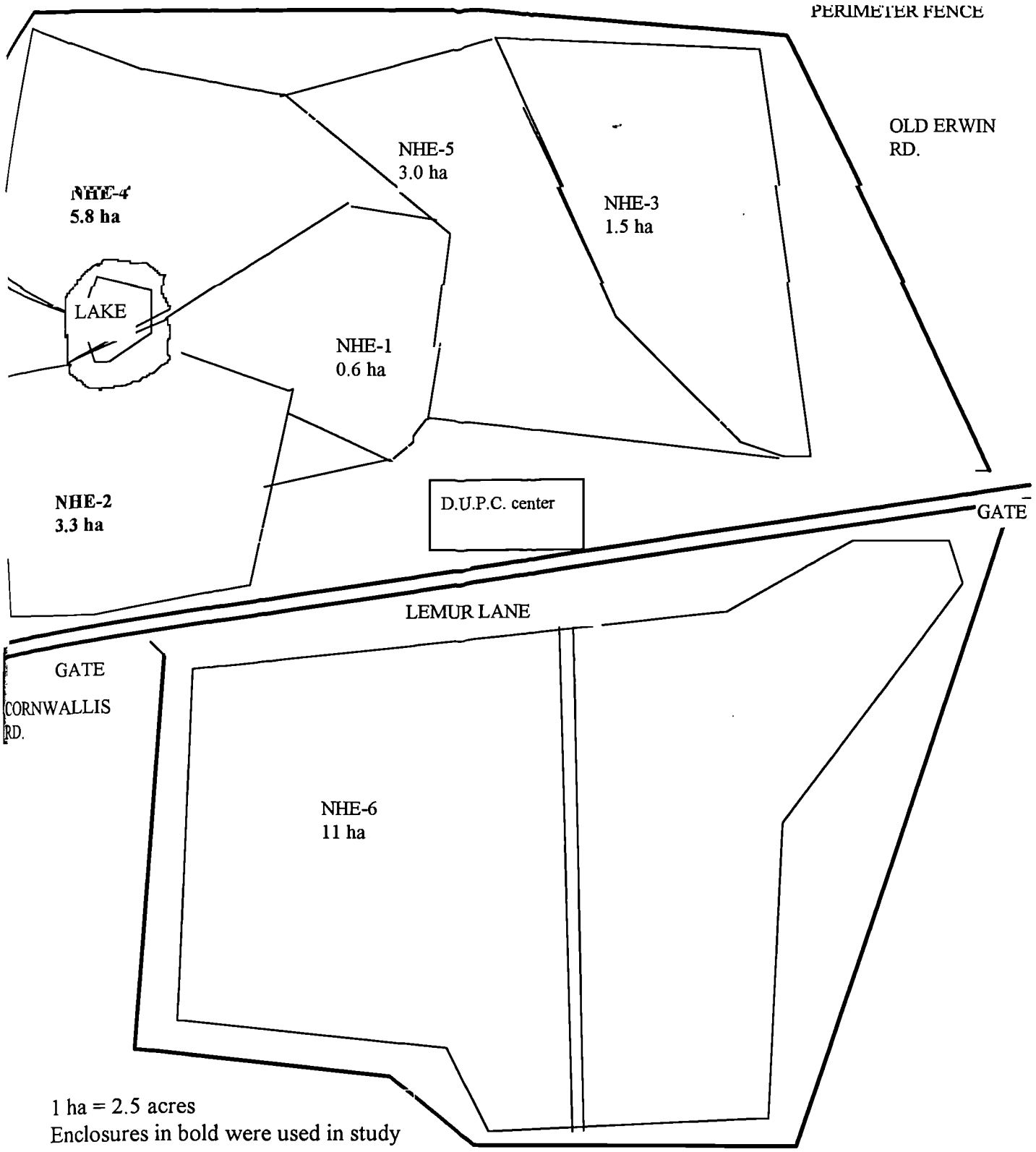


Fig. 3.1: Duke University Primate Center, lemur enclosures.

Figure 3.2: *Lemur catta* at DUPC

Figure 3.3: *Eulemur fulvus rufus* at DUPC

Name	Sex	D.O.B.	Identification		Site	F	B
			Collar	Tag			
Cercolas	m	'83	blue		NHE-2		
Corinna	f	'83	brown	gold triangle	NHE-2	*	
Selacius	m	'85		limp	NHE-2		
Lycus	m	'85	lt. blue	gold L	NHE-4	*	*
Katina	f	'87	brown	orange cross	NHE-2		
Nemo	m	'87	dull yellow	gold scrotum	NHE-2		
Ninna	f	'89	yellow	black circle	NHE-2	*	
Hector	m	'89	yellow	orange diamond	NHE-2		
Aeschylus	m	'90	red	red bone	NHE-2		
Gelon	m	'91	black	silver hydrant	NHE-2		
Adea	f	'93	pink	purple heart	NHE-2	*	
Licinius	m	'93	pink	gold pentangle	NHE-2		
Thessalus	m	'93	pink	silver bone	NHE-2		
Nikandros	m	'94	blue	purple clover	NHE-2	*	
Nanno	m	'94	blue	green illinois	NHE-2	*	
Alexandra	f	'95			NHE-2		
Katina's baby		'96			NHE-2		
Corinna's baby		'96			NHE-2		
Ninna's baby		'96			NHE-2		
Cleis	f	'85	lt. blue	orange clover	NHE-4	*	*
Cleomenis	f	'85	lt. blue	blue pentagon	NHE-4		
Agnostes	m	'87			NHE-4	*	*
Dory	f	'89	yellow	gold zigguret	NHE-4	*	*
Alice	f	'89	yellow	blue Michigan	NHE-4	*	*
Nestor II	m	'90	black	green bell	NHE-4	*	
Seuthes	m	'91	red	blue circle	NHE-4	*	
Aracus	m	'91	red	green octagon	NHE-4	*	*
Philocles	m	'92	blue	blue flower	NHE-4	*	*
Thyrea	f	'93	pink	gold star	NHE-4	*	*
Charissa	f	'94	blue	red Ohio	NHE-4	*	*
Cassandra	f	'94	blue	gold Michigan	NHE-4	*	*
Charops	m	'94	blue	green rectangle	NHE-4	*	*
Cercops	m	'95	green	blue cross	NHE-4	*	*
Teres	m	'95	green	purple cat	NHE-4	*	
Valgius	m	'95	green	blue shield	NHE-4	*	*
Stephanus	f	'95		in treatment, sick	NHE-4		
Thyrea's baby		'96			NHE-4		
Cleomenis's baby		'96			NHE-4		

D. O. B.: Date of birth
F: faecal samples collected
B: reflectance measurements made using spectrophotometer

Table 3.1: *Lemur catta* individuals at DUPC

Name	Sex	D.O.B.	Identification		Site	F	B
			Collar	Tag			
Sorrel	m	'80	brown	silver shield	NHE-2	*	*
Flare	f	'86	red	gold triangle	NHE-2	*	
Rory	m	'89	lt. blue	yellow hydrant	NHE-2	*	*
Rosella	f	'92	short tail		NHE-2	*	*
Redoak	m	'93	black	green heart	NHE-2	*	*
Redbay	f	'95			NHE-2	*	*
Reddevil	infant	'96			NHE-2		*
Redlake	f	'83	lt. blue	blue shield	NHE-4	*	*
Akako	m	'87	green	blue heart	NHE-4	*	
Rage	m	'89	purple	red kennel	NHE-4	*	
Carmine	m	'92	black	silver rectangle	NHE-4	*	*
Redwood	f	'94			NHE-4	*	*
Strawberry	f	'94	red	gold circle	NHE-4	*	*
Cardinal	m	'95			NHE-4		
Redlake's baby		'96			NHE-4		

D. O. B.: Date of birth
F: faecal samples collected
B: brightness measurements made using spectrophotometer

Table 3.2: *Eulemur fulvus rufus* individuals at DUPC

3.2 Faecal collection

The samples were collected over the summer before the animals were given their annual dose of Milbemycin for warble fly infestation, the veterinary surgeon confirmed that this drug may have a small effect on intestinal parasites. At the DUPC lemur infants are born between March and June, after a gestation priod of 120-135 days.

Faecal samples were collected for known individuals and analysed to calculate the endoparasitic load by making worm and oocyte counts (Stuart & Strier, 1995). The samples were initially collected from both species for as many individuals as possible; after a week of collection, certain individuals were selected for faecal collection. This method of collection served two purposes; the first was to practice faecal collection identifying common defecating sites, and the second was to identify the individuals that were less wary and therefore easier to collect samples from, by following specific individuals in their everyday routine.

3.21 Collection Routine

Faecal collection was made in the forest enclosures NHE-2 and NHE-4 between 8.30am and 4pm, when the lemurs were most active. The lemurs fed on tree leaves and insects, but were also fed a supplement food of monkey chow. This was distributed around the forest at around 2pm by a DUPC technician wearing a white lab coat. This helps the lemurs to associate feeding with the white coat and not to expect food from humans who are not wearing white. To enforce the white coat associative programming, researchers

wear drab coloured clothes. Latex gloves were worn while collecting the faecal samples. The majority of collections were made in the morning before feeding. Small samples of fresh stool were collected immediately after defecation, which reduces external parasite contamination. The samples were picked up using a clean tongue depressor and placed in plastic bottles with screw top lids containing formalin neutral buffered pH 7.0 Gurr with 4% formaldehyde. This preserves the eggs and worm tissue from dessication and denaturation for up to six months (Stuart and Strier, 1995). The sample bottles were stored in a large lockable plastic container during transit. After the collection of each sample, the time, date, faecal consistency, presence of visible worms and the identification of the individual were noted and the sample numbered for the examination. In total 140 faecal samples were collected, 25% of which could not be used due to the lack of brightness data available for specific individuals. As many samples as possible were collected for the chosen individuals but the sample size varied between one and ten due to the problems of faecal collection in a constrained time limit.

3.22 Faecal samples from wild and captive animals

The DUPC faecal samples were collected from free ranging, but captive animals, so it was necessary to compare parasite loads from DUPC lemurs with lemurs in the wild, and in zoo captivity. By comparing the parasite loads with the loads used to test the bright male hypothesis, an assessment could be made of the validity of parasite loads from free ranging, but captive individuals. If the parasite infection is similar between the wild and free-ranging captive lemurs, then the loads would be acceptable. If, however the loads from the DUPC lemurs are more similar to the zoo lemurs, then the conditions under

which the lemurs were tested must not mimic the natural environment sufficiently to have a "normal" parasite population.

Faecal samples were collected from two individuals at London Zoo, one *Eulemur macaco* and one *Varecia varecia* lemur. Unfortunately, no *Lemur catta* or *Eulemur fulvus rufus* species are housed at London Zoo for faecal collection. This should not affect the results and validity of the comparison as the species are found in a similar environment and the *Varecia* sp. were sharing the same enclosure as both of the lemur species tested at DUPC. One fresh sample was collected from the cage floor for each species at the zoo using the methods discussed above.

Faecal samples were also collected from the wild from the Beza Mahafaly Special Reserve in Madagascar, July 1995 and kindly donated by Dr M. Sauther from Colorado University. Over twenty faecal samples were provided from known *Lemur catta* individuals preserved in 70% alcohol and stored in glass vials. Some of the samples were too small to analyse effectively as the majority of a small sample was vegetative material such as leaves and twigs. Thirteen samples however, were analysed as in the methods described below (see Appendix 3.2).

3.3 Faecal Examination

Training in parasitology was provided by Dr MacGregor of the Zoological Society of London based at London Zoo, Regents Park. Examination of the sample faeces was conducted in the Department of Anthropology at Durham University. Samples were

analysed in a Grade B fume cupboard wearing latex gloves, a mask, safety goggles and a laboratory coat. All samples were examined by number alone, only after faecal analysis was complete were the samples linked to individuals.

3.31 Worm identification and counts

The first stage of calculating the gut parasite load of an individual was to count the visible worms in each faecal sample. This was conducted by emptying an individual sample into a white sterile disposable dish and searching through the vegetative material using a wooden stirrer. The worms identified were up to 4mm long and were easily visible under a strong light. After each sample was examined for parasitic worms, it was returned to the plastic vial until the oocyte (egg) counting process. Representative worms were mounted on slides and viewed under a light microscope under x100 and x250 magnification for species identification. The worms were photographed in the Biological Sciences department at the University of Durham using a transmission microscope with attached camera (see Results). Professor Gibbons, the Head of the Animal Helminthology Biosystematics Unit at the International Institute of Parasitology, Hertfordshire, made final confirmation of species identification.

3.32 Oocyte Identification and counts using the McMasters Method

The second stage of calculating an individual's endoparasite load required making counts of worm oocytes (eggs) present in the faeces. This was performed using the McMasters

method (Thienpont *et al.*, 1986). Two grams of the faecal sample is removed from the formalin solution and the suspension sieved using a tea strainer. The smaller particles are washed through the sieve using 60ml of saturated sodium chloride solution, made using one NaCl tablet in 500ml distilled water. The strained liquid was stirred to re-suspend the particles and homogenise the concentration of oocytes throughout the liquid. A glass pasteur pipette is used to fill the chamber of a counting slide. The compartment has a volume of 0.15ml as the surface is 10 x 10mm with a depth between the cover slide and base of 1.5mm. The cover slide is etched to give a $100mm^2$ area, within which the oocytes are counted. Two compartments are counted to accurately assess the number of oocytes per faecal sample. A light microscope at x100 magnification is used to perform the counts, and species identification was made at x250 magnification. The number of oocytes counted in the 0.15ml volume corresponds to the concentration of faeces, 1g in 30ml.

The mean of the two oocyte counts is used to calculate the number of oocytes (eggs) per gram (EPG). The EPG can be calculated using the following equation:

EPG = n x 200

When 2g faeces is dissolved in 60ml sodium chloride solution and n = number of oocytes counted in one counting compartment

Identification of parasitic oocytes was successful for only three of the parasite species using parasite identification references (Thienpont *et al.*, 1986; Ash & Orihel, 1987; Fiennes, 1967; Soulsby, 1967; Fowler, 1993). No further identifications could be made

by the Animal Helminthology Biosystematics Unit at the International Institute of Parasitology, Hertfordshire. Photographs were also taken of the parasite oocytes and worms (see Results).

3.4 Measuring reflectance

Reflectance was used to identify and compare colouration differences between individuals. It is a more appropriate measure of pelage colour variation because assessing variation using a visual scale is inaccurate, and biased by the observer assessing the nature of the colours. The spectrophotometer also identifies very small variations in reflectance (0.05%), which allows for accurate discrimination of the intensity of pelage colour between individuals. Two days were spent measuring the pelage brightness of individual lemurs at DUPC. The measuring process was made to coincide with veterinary check-ups for the two species to minimise the lemur's distress. Measuring pelage reflectance involved netting lemurs individually, and holding them in a storage pen enabling reflectance measurements to be taken using the spectrophotometer. Two technicians were required to help capture the animals with a net, and to hold the lemurs while measurements were taken (Fig. 3.3). The reflectance was measured for each netted individual on the same six body parts that were measured on skins at the Natural History Museum, London. Two readings were made for each body part to account for measurement error and the mean reflectance calculated (see Appendix 3.1). The whole measurement process was limited to a few minutes for each individual and the mothers with infants were captured together to reduce stress. Due to the open natural forest, it was impossible to capture all of the lemurs for which faecal samples were collected and,

therefore, many of the faecal samples could not be used without the complimentary brightness data.

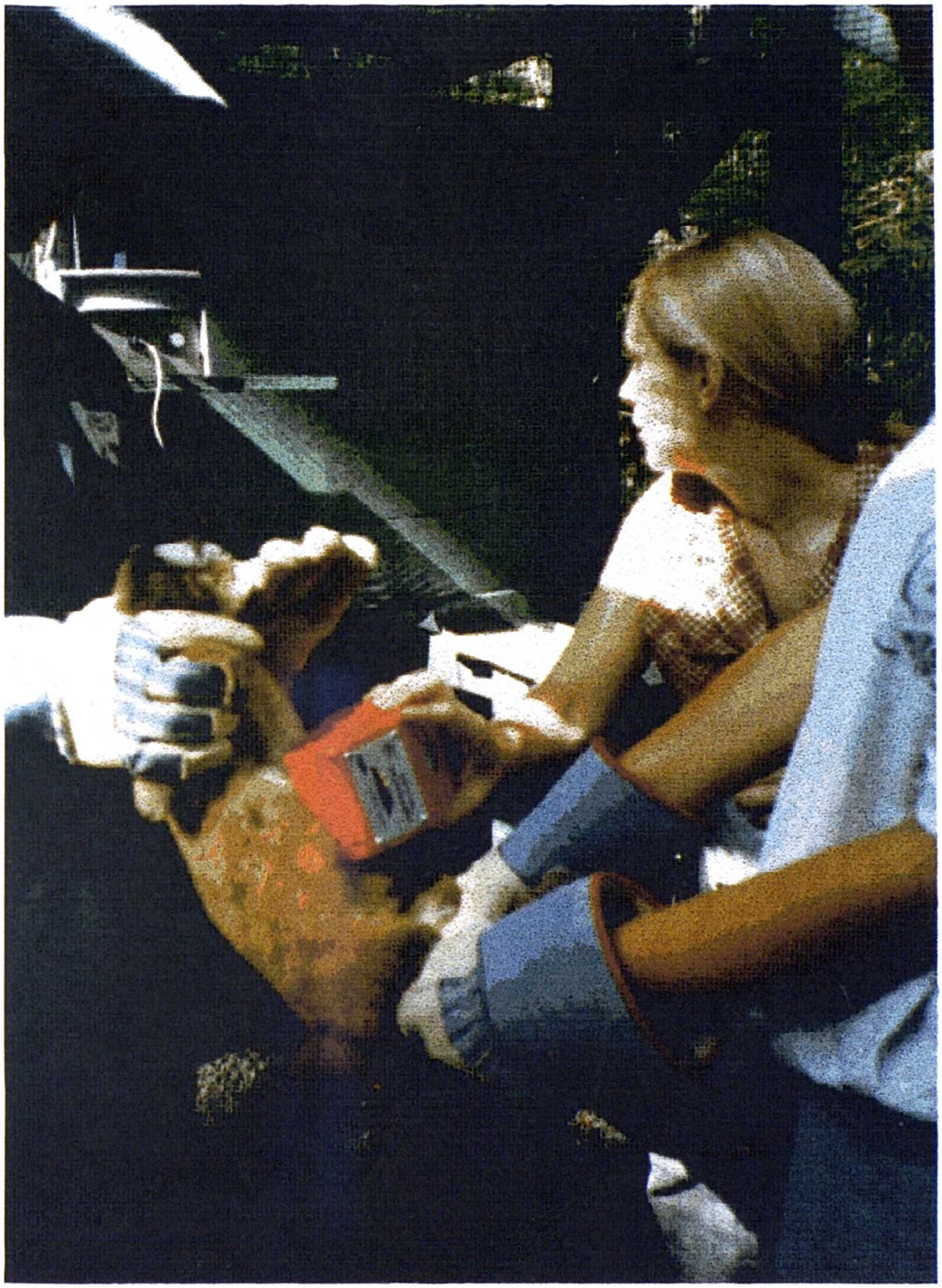


Figure 3.4: Measuring the reflectance of *Eulemur fulvus rufus* using the reflectance spectrophotometer

3.5 Calculating Worm and Oocyte load

When assessing the parasitic load of an individual lemur, the worm number and oocyte number were considered separately. This allows for the variation in parasite forms, dependent on the stage in the parasite lifecycle at the time of collection. The parasitic worms were counted from samples where there was brightness data available. Worms were classified, if possible and the average load calculated for each species to account for the variation in sample numbers between individuals. The average oocyte load of an individual was calculated using the same method. Six parasite species were found, although not all were classified.

The parasite data used for statistical analysis is given in Appendix 3.1. Average load was described in terms of each parasite and the form (oocyte or worm) for which they were identified. In total eight columns of parasite load data were used for analysis.

3.6 Comparing endoparasite load with pelage brightness

Brightness measurements were taken for each individual on six different body parts, with the average from two measurements of body area used for the analysis (Appendix 3.1). In addition to comparing the brightness measurements of an individual's body parts, total brightness was calculated by summing the reflectance measurements of each body part. This gave a broad range of continuous reflectance measurements, enabling direct comparisons to

be made for overall pelage brightness between individuals and species.

Statistical comparisons were made between various measurements of parasite load and pelage brightness using the Apple Macintosh package Statview 4. One-tailed tests of the predicted negative relationship between loads and brightness were made using linear regression. Results were only recorded for an individual lemur's total brightness, crown and chest brightness (the two pelage areas in which the brightness was most variable between individuals). Parasite counts were also made on samples collected from wild and captive lemurs. Faecal analysis and parasite counts were necessary as a form of control for the free ranging state of the two lemur species studied (App. 3.2).

Chapter 4

Results (part one)

4.1 Taxonomic distribution of character states

The first stage of this study was to look at how species characteristics are distributed, to identify evolutionary trends throughout the order. Table 4.1 shows the distribution of sexual dichromatism and natal colouration arranged taxonomically in nocturnal and diurnal primates. Nocturnal species appear only in the more "primitive" suborder, the Strepsirhini, with the exception of *Aotus trivirgatus* (the night monkey), which is in the Platyrrhini, and the tarsier. Throughout the primates, nocturnal species do not exhibit sexual dichromatism or natal colouration (Table 4.1). For diurnal species, both strepsirhines and haplorhines exhibited natal colouration and sexual dichromatism. The Hominoidea have the greatest proportion of species displaying sexual dichromatism (attributable to the gibbons), and the greatest proportion of species with natal colouration. The catarrhines however, have the most species displaying natal colouration with 36 species out of 66 analysed (54%), which is the same proportion of species as the Hominoidea. This indicates that sexual dichromatism is mainly a feature of strepsirhines (42%) and hominoids (31%), where the percentage of species displaying sexual dichromatism is similar in the cercopithecoids (11%) and platyrrhines (5%). Natal colouration is common in cercopithecoids (54%) and hominoids (54%) and present, but at a lower frequency in strepsirhines (8%) and platyrrhines (10%). Over the 130 diurnal primates analysed throughout the order, 14% display sexual dichromatism and a much higher 37% of the species display a natal colouration. Two-way tables and the test of independence were used to determine taxonomic correlations with colour variation for sexual dichromatism or natal colouration. This method was also used to demonstrate pitfalls caused by comparing species data without accounting for phylogeny.

SUBORDER STREPSIRHINI - 37 species

Features present	% of total		Tot. No.
	NOCTURNAL 25 sp.	DIURNAL 12 sp.	
Sex. dichromatism	0	42	5
Natal colouration	0	8	1

SUBORDER HAPLORHINI
INFRAORDER PLATYRRHINI - 40 species

Features present	% of total		Tot. No.
	NOCTURNAL 1 sp.	DIURNAL 39 sp.	
Sex. dichromatism	0	5	2
Natal colouration	0	10	4

SUPERFAMILY CERCOPITHECOIDEA - 66 species

Features present	% of total		Tot. No.
	NOCTURNAL 0 sp.	DIURNAL 66 sp.	
Sex. dichromatism	-	11	7
Natal colouration	-	54	36

SUPERFAMILY HOMINOIDEA (excluding *Homo sapiens*) - 13 species

Features present	% of total		Tot. No.
	NOCTURNAL 0 sp.	DIURNAL 13 sp.	
Sex. dichromatism	-	31	4
Natal colouration	-	54	7

% TOTAL FOR DESCRIPTIVE STATES FOR 156 PRIMATE SPECIES

Features present	% of total		Tot. No.
	NOCTURNAL 26 sp.	DIURNAL 130 sp.	
Sex. dichromatism	0	14	18
Natal colouration	0	37	48

Table 4.1: Distribution of colouration states in the order Primates

4.2 Two-way tables and the test of independence

Table 4.2 displays the result of the analysis of 14 two-way tables (tables given in Appendix 2.1) calculated using the test of independence (Sokal & Rohlf, 1981). To be considered a statistically significant result (the two variables tested are correlated), the value for *G* adj. must be of a greater value than the value for $\chi^2_{.05[1]} = 3.841$.

Two-way tables 1-7, testing for associations between sexual dichromatism and natal colouration with breeding system, size dimorphism and each other, include 26 nocturnal species. Results indicate that six of the seven hypotheses should be rejected. Only natal colouration was found to correlate with sexual size dimorphism (Table 4.2, no. 5). When the seven tests are repeated omitting the nocturnal species, there were no correlations with sexual dichromatism. Contrary to the results including nocturnal species no correlation exists between sexual size dimorphism and natal colouration in diurnal species (Table 4.2, no. 5). There is however, a correlation between natal colouration and multi-male mating system in diurnal species (Table 4.2, no. 6); although no correlations were found between natal colouration or sexual dichromatism with each other, a single male mating system or sexual size dimorphism. It should be noted that tests involving single male and multi-male comparisons will not give complementary results as monogamous family groups are also considered in each comparison for example, species which are not classed as single male are either multi-male or monogamous family-grouped species. These results indicate that sexual dichromatism is not associated with any of the variables tested (natal colouration, sexual size dimorphism or mating system). Therefore, with respect to sexual dichromatism, no

hypotheses can be accepted and hypotheses 1-4 must be rejected. Natal colouration is associated with a multi-male mating system only when the nocturnal species are removed. Therefore, hypothesis 6 is accepted and hypotheses 4 and 5 must be rejected. Conflicting results when the nocturnal species are included or excluded illustrate that the inclusion of nocturnal species in the two-way comparisons alters the expected results, as only diurnal species showed intraspecific pelage colour variation. Only one of the seven hypotheses is supported when using two-way tables and the test of independence. The meaning and implications of these results will be considered in the discussion.

	Diurnal & Nocturnal species (n=156)		Diurnal species only (n=130)	
Hypotheses	*G*adj	Significance	*G*adj	Significance
1. Sex. dich. is associated with natal colouration	-5.78	NS	2.89	NS
2. Sex. dich. is associated with sexual size dimorphism	0.16	NS	0.31	NS
3. Sex. dich is associated with mating system, single male	0.80	NS	1.90	NS
4. Sex. dich. is associated with mating system, multimale	0.68	NS	2.93	NS
5. Natal colouration is associated with sexual size dimorphism	8.38	*	1.65	NS
6. Natal colouration is associated with mating system, multimale	0.50	NS	5.88	*
7. Natal colouration is associated with mating system, single male	0.01	NS	0.89	NS

$\chi^2_{0.5[1]} = 3.841$
* = significant at $p < 0.05$ (this obtains when Gadj > 3.841 for association)
NS = not significant (when Gadj < 3.841 for independence)
N.B.: Hypotheses in bold indicate conflicting results when nocturnal species are included

Table 4.2 Tests of independence using two-way tables

4.3 Interspecific Comparative Analysis by Independent Contrasts

The analysis was divided into four parts:

1. To determine ecological and behavioural correlations with sexual dichromatism and the pelage colour brightness of each
2. To determine associations with ecological and behavioural variables and brightness, but using reflectance measurements
3. Comparing brightly coloured genitalia and ornamentations with the ecological and behavioural variables
4. To determine ecological and behavioural correlations with natal pelage colouration

4.31 Interspecific correlations with sexual dichromatism and pelage brightness

Table 4.3 shows the results of regression (through the origin) and one-sample *t*-tests performed on outputs from CAIC corresponding to each comparison. Five tests were performed (data sets listed in Appendices 1.2-1.5) to identify correlations with sexual size dimorphism (coded as 1) and average group size (coded as 2), and male, female and natal brightness. Other variables could not be compared in CAIC as they were discrete variables. Neither group size nor sexual size dimorphism were correlated with sexual dichromatism (comparisons of variables 1 D and 2 D). To consider pelage brightness (Table 4.3,

comparisons D A, D B, and D C), neither male nor female pelage brightness was significantly correlated with sexual dichromatism. Hence, overall reflectance is not a measure of sex differences in colouration (see section 4.32). Infants show a trend to be brighter in species that display sexual dichromatism (Table 3.3, D C).

The continuous brightness scale attributed to male and female pelage was compared with all eight ecological and behavioural variables. Polygamy and diurnality were significantly correlated with a bright male pelage (Table 4.3, comparisons 5 A and 8 A). For female brightness, there is a significant correlation with polygamy (Table 4.3, comparison B 5) and there is a trend with group size (Table 4.3, comparison B 2).

4.32 Interspecific correlations with sexual dichromatism and reflectance measurements

Table 4.4 gives the statistical results when reflectance measurements were compared with sexual dichromatism and seven of the ecological and behavioural variables. Reflectance measurements are mostly for the rump and chest regions of the pelage. When there seemed to be a significant correlation, other body parts were also used in the comparison. Sexual dichromatism significantly correlated with a reflectant chest in both the male and female (Table 4.4, comparisons G D and G E). Interestingly, the results show that males of dchromatic taxa had less reflectant chests, and females had more reflectant chests than in non-dichromatic taxa. Male reflectance showed only a trend with a reflectant rump region

and male dominance. Mean female reflectance is negatively correlated with dimorphism, a result largely attributable to rump reflectance, but also reflected in trends for the other body parts (Table 4.4, comparisons 3 E). Multi-male grouping and male dominance also showed a trend of correlation with female reflectance (Table 4.4, comparisons 4 E and 7 E). A non-significant trend is present in the relationship between female reflectance and mating system (females are more reflectant in multi-male taxa).

4.33 Interspecific correlations with female ornamentations and bright genitalia

In species displaying bright genitalia, both male and female pelage brightness correlate negatively with bright genitalia (males and females are duller in species with bright genitalia, Table 4.5, comparison 5 A and 5 B). Dull male rumps show a trend with bright genitalia (Table 4.5, comparison 5 G). Here, dull pelages may have evolved to maximise colour contrast, hence the conspicuousness of bright genitalia. Size dimorphism and group size does not correlate with bright genitalia (Table 4.5, comparisons 5 2, and 5 3). The overall reflectance of male and female pelage does not correlate with the possession of bright genitalia (Table 4.5, comparisons 5 D, and 5 E). Comparisons with female ornamentations show no correlation with male and female brightness or reflectance, average group size and size dimorphism (Table 4.5). Male overall reflectance is significantly correlated with female ornamentation, where males are significantly duller in female ornamented taxa (Table 4.5, comparison 4 I). There is a trend with male rump reflectance, where the rumps are brighter in species showing female ornamentations (Table 4.5, comparison 4 G).

4.34 Interspecific correlations with species displaying natal colouration

Table 4.6 is divided into two parts, the first compares natal colouration, brightness and reflectance with the eight ecological and behavioural variables, and the second compares natal brightness and the presence of a natal pelage with the occurrence of female ornaments or bright genitalia. In part 1, both male and female brightness positively correlate with the presence of natal colouration (Table 4.6, comparisons E A and E B). Natal colouration is not associated with size dimorphism or average group size (Table 4.6, comparisons E 1 and E 2). Not surprisingly, natal colouration is strongly correlated with natal pelage brightness (Table 4.6, comparison E C). Natal brightness does not correlate with any of the eight socio-ecological variables, but shows a trend with sexual dichromatism (Table 4.6, comparison D C). Natal reflectance shows no correlation with sexual dichromatism or natal colouration (Table 4.6, comparisons G F, H D, and H E). Neither female ornamentation nor bright genitalia correlate with natal brightness or reflectance (Table 4.6, comparisons 9 C, 9 F, 10 C, and 10 F).

Variables		*n* species	*p*	*t*	*df*	Significance
1)						
1	D	113	.17	-1.52	8	NS
2	D	81	.35	-1.00	7	NS
D	A	132	.65	.47	10	NS
D	B	132	.71	-.39	10	NS
D	C	132	.06	2.11	10	+
1	A	113	.27	-1.10	98	NS
2	A	81	.11	1.64	68	NS
4	A	109	.48	-.72	15	NS
5	A	114	.05	2.15	11	*
6	A	122	.50	.71	8	NS
7	A	128	.59	-.60	3	NS
8	A	158	.05	3.20	3	*
1	B	113	.77	-.29	98	NS
2	B	81	.06	1.92	68	+
4	B	109	.75	-.32	15	NS
5	B	114	.05	2.14	11	*
6	B	122	.60	.55	8	NS
7	B	128	.59	-.60	3	NS
8	B	158	.14	1.98	3	NS

NOTES: 1 = % Male weight
2 = Av. group size
3 = Size dimorphism
4 = Multimale grouping
5 = Polygamy
6 = Terrestriality
7 = Male dominance
8 = Diurnality

A = Male colour brightness
B = Female colour brightness
C = Natal colour brightness
D = Sexual dichromatism

p = *p* value
t = *t* value
df = degrees of freedom

* $p \leq 0.05$
+ $p \leq 0.1$

Table 4.3: Comparative analysis results for sexual dichromatism using colouration data

Variables 1)		*n* species	bodypart	*p*	- *t*	*df*	Significance
G	D	40	iii chest	.01	-3.88	6	*
			vi rump	.17	1.55	6	NS
G	E	38	iii	.04	2.55	6	*
			vi	.50	.71	6	NS
2	D	30	vi	.98	.02	27	NS
3	D	40	vi	.27	-1.35	3	NS
4	D	28	vi	.31	1.13	5	NS
5	D	36	vi	.55	-.65	4	NS
6	D	36	vi	insufficient contrasts			
7	D	39	vi	insufficient contrasts			
2	E	29	vi	.54	.63	26	NS
3	E	38	i crown	.09	-2.55	3	+
			ii cheek	.08	-2.63	3	+
			iii chest	.16	-1.81	3	NS
			iv back	.10	-2.34	3	+
			v outer leg	.10	-2.31	3	+
			vi rump	.00	-8.54	3	*
			vii mean	.03	-3.90	3	*
4	E	26	vi	.07	2.26	5	+
5	E	34	vi	.45	-.83	5	NS
6	E	35	vi	insufficient contrasts			
7	E	37	vi	insufficient contrasts			

NOTES: 1 = % Male weight
2 = Av. group size
3 = Size dimorphism
4 = Multimale grouping
5 = Polygamy
6 = Terrestriality
7 = Male dominance

D = Male reflectance
E = Female reflectance
G = Sexual dichromatism

p = *p* value
t = *t* value
df = degrees of freedom

* $p \leq 0.05$
+ $p \leq 0.1$

Table 4.4: Comparative analysis for sexual dichromatism using reflectance colouration data.

Variables		*n* species	*p*	*df*	Significance
4	A	158	.30	5	NS
4	B	158	.30	5	NS
4	1	138	.40	3	NS
4	2	90	insufficient contrasts		
4	3	158	.36	5	NS
4	D	158	.33	5	NS
4	E	39	insufficient contrasts		
4	G	41	.06	4	+(-ve)
4	H	39	.27	4	NS
4	I	41	.03	3	*(-ve)
4	J	39	.87	3	NS
5	A	158	.05	3	*(-ve)
5	B	158	.04	3	*(-ve)
5	1	138	.48	5	NS
5	2	90	.23	6	NS
5	3	158	.61	14	NS
5	D	39	.34	3	NS
5	E	39	.30	3	NS
5	G	44	.06	3	+ (-ve)
5	H	42	.27	3	NS

NOTES: 1 = % Male weight
2 = Av. group size
3 = Size dimorphism
4 = Fem. ornamentation
5 = Bright genitalia

A = Male colour brightness
B = Female colour brightness
D = Male mean reflectance
E = Female mean reflectance
G = Male rump reflectance
H = Female rump reflectance
I = Male chest reflectance
J = Female chest reflectance

$p = p$ value
$t = t$ value
df = degrees of freedom

* $P \leq 0.05$
$^{+}P \leq 0.1$

Table 4.5: Comparative analysis results with the presence of female ornamentations and bright genitalia

Variables		*n species*		*p*	*t*	*df*	Significance
1)							
E	A	132		.05	2.07	21	*
E	B	132		.01	2.75	21	*
E	1	113		.90	.12	20	NS
E	2	81		.41	.84	15	NS
E	C	132		.00	4.37	21	*
1	C	113		.63	-.49	98	NS
2	C	81		.87	.16	68	NS
4	C	109		.43	.80	15	NS
5	C	114		.43	.81	15	NS
6	C	122		.44	.82	8	NS
7	C	128		.58	-.62	3	NS
8	C	158		.11	2.16	3	NS
D	C	132		.06	2.11	10	+
H	D	40	iii chest	.95	.06	6	NS
			vi rump	.92	-.10	6	NS
H	E	38	iii chest	.65	.48	6	NS
			vi rump	.43	-.84	6	NS
2)							
9	C	158		.24		5	NS
10	C	158		.26		3	NS
9	F	23			insufficient contrasts		
10	F	23			insufficient contrasts		

NOTES: 1 = % Male weight
2 = Av. group size
3 = Size dimorphism
4 = Multimale grouping
5 = Polygamy
6 = Terrestriality
7 = Male dominance
8 = Diurnality
9 = Fem. ornamentation
10 = Bright genitalia

A = Male colour brightness
B = Female colour brightness
C = Natal colour brightness
D = Sexual dichromatism
E = Natal colouration
F = Natal total reflectance
H = Natal reflectance

p = *p* value
t = *t* value
df = degrees of freedom

* $P \leq 0.05$
+ $P \leq 0.1$

Table 4.6: Comparative analysis results for natal colouration using pelage colouration and reflectance measurements

4.4 Comparisons of reflectance measurements with colour

While measuring the reflectance of pelages at the Natural History Museum, London, it became apparent that, unlike the assessment of brightness using the visual scale, a high reflectance did not necessarily correspond with a bright pelage colouration. Three diagrams are included in this section to show how reflectance measurements, pelage colour and brightness measurements corresponded to one another. Figure 4.1 shows how the reflectance varied with pelage colouration for the 47 species sampled. In general blacks, browns, and dull looking colours gave a low reflectance, as would be expected, between 1-5%. Surprisingly orange, ginger, yellow, gold, and blue also gave a low reflectance. For example, the pelage of the golden lion tamarin, *Leontopithecus rosalia,* was visually assessed and awarded a brightness of 3, yet the mean reflectance was 27.3%.

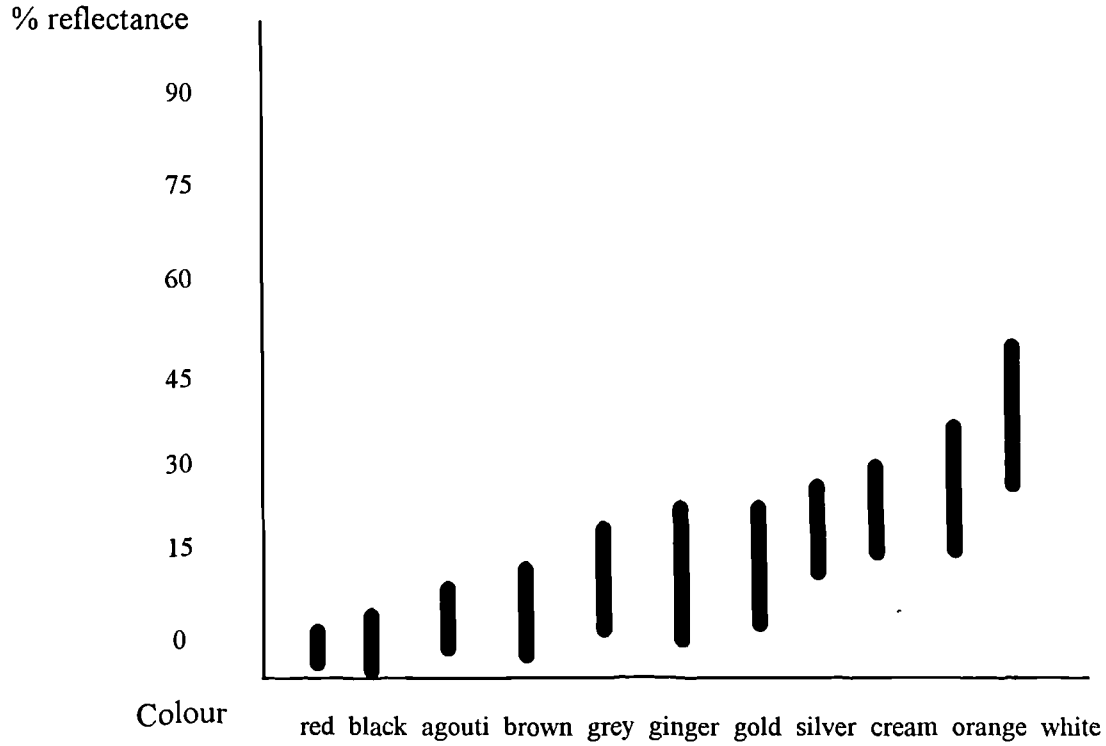


Figure 4.1: Pelage colourations with reflectance measurements

Figure 4.2 shows the distribution of the visually assessed pelage brightness with colour. Colours such as black, white, gold and orange are considered to be bright and are awarded a 3. Black may not seem a typical colour to be described as bright, but an all over black shiny pelage, as in male *Lemur macaco,* is very striking and highly visible in an arboreal habitat. Browns and agouti-type pelages are considered to be a dull colouration and awarded a 1. Neutral colours such as grey, cream and silver are awarded a 2 as they were considered to be neither dull nor bright.

Figure 4.3 compares the distribution of pelage reflectance with pelage brightness measurements for the 47 species sampled. There is an uneven distribution between pelage reflectance and visual brightness. Reflectance measurements only correlate with brightness category, at the highest reflectances. Therefore, there is no direct relationship between the two forms of measuring pelage colouration and both will be considered as separate entities. The standard deviation of pelage reflectance was calculated from five individual skins for three species, and compared to the standard deviation between the mean pelage reflectance for the three species. The intraspecific variation in pelage reflectance was larger than the interspecific pelage reflectance variation (see Appendix 1.11).

A Mann-Whitney U test was performed between the reflectance measurements of dead and live *Lemur catta* pelage considering each body part seperately (Siegal and Castellan, 1988). Body part reflectance measurements for ten live individuals and two dead museum specimens did not reach significance indicating that the reflectance measurements compare well with that of live animals (Appendix 1.13). Therefore, the use of reflectance

measurements from museum specimens that have been carefully preserved is justified as an accurate measurement of actual pelage reflectance.

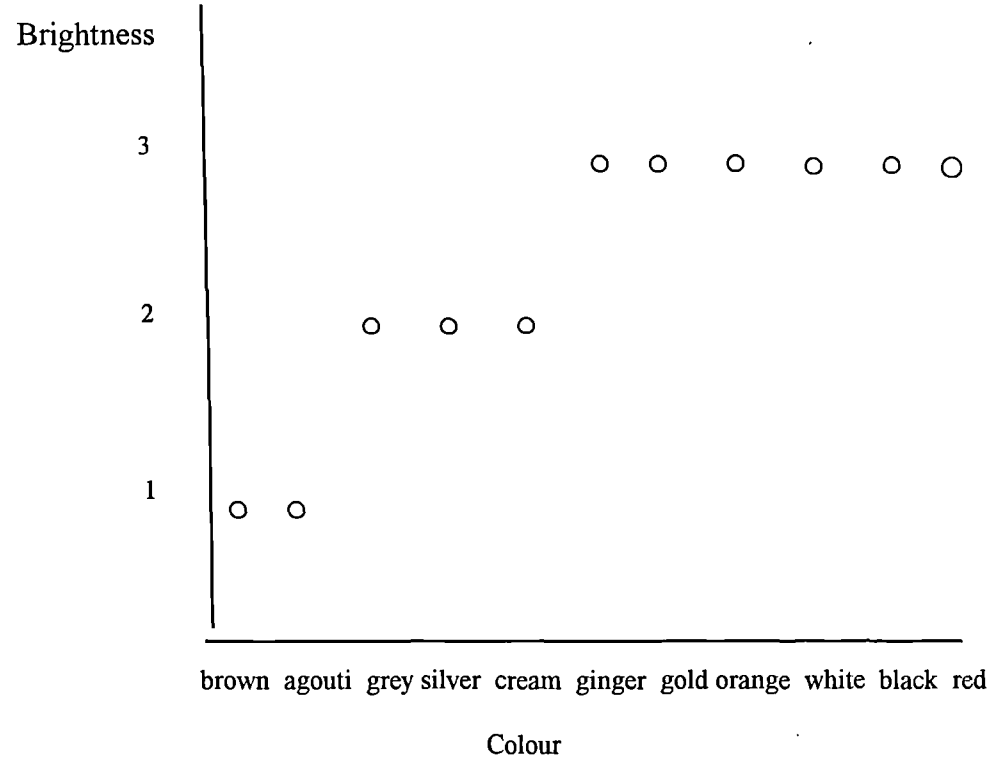


Fig. 4.2: Pelage colourations with pelage brightness scores

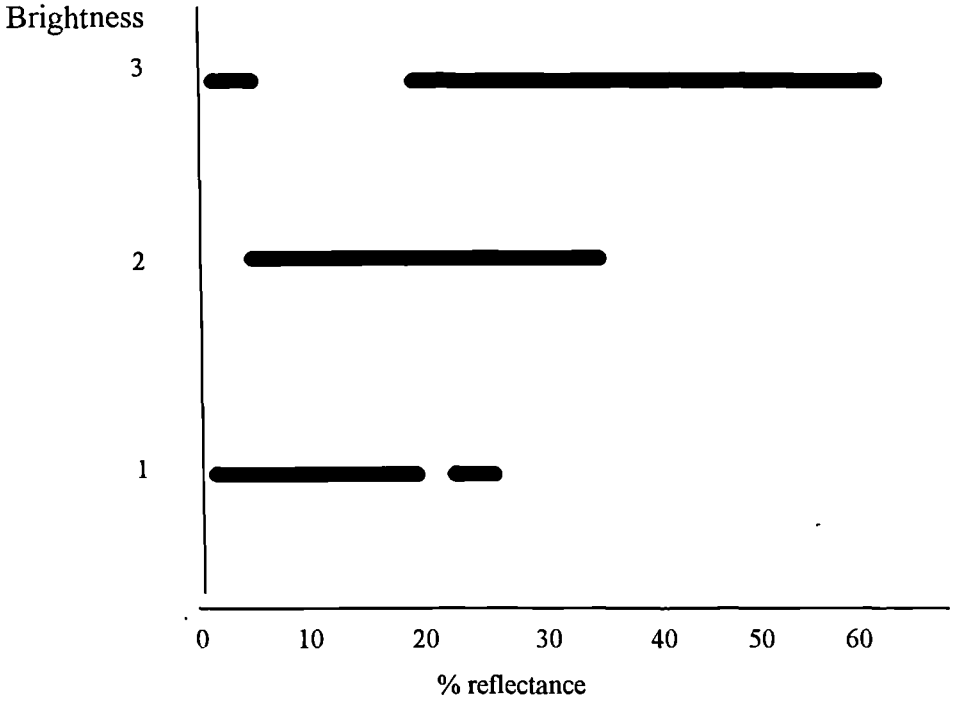
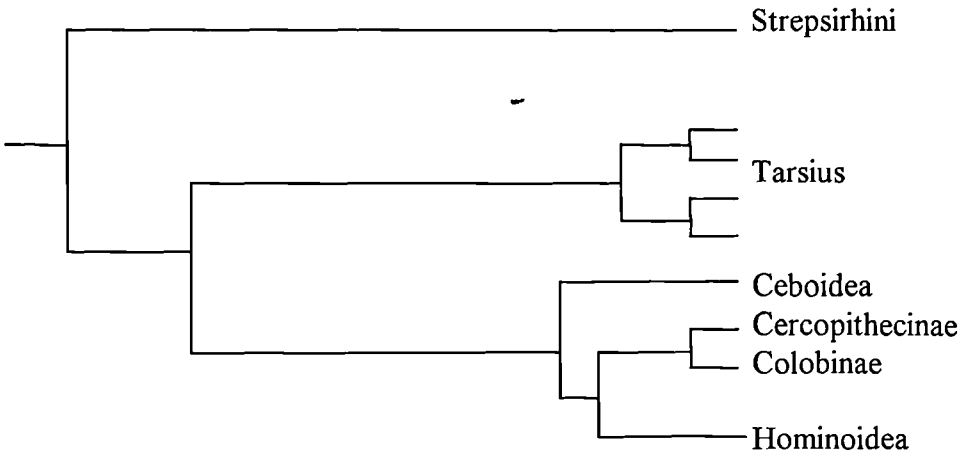


Fig. 4.3: Comparison of reflectance measurements with brightness scores

4.5 Comparative analysis using the binary method

Tests that could not be performed using CAIC were analysed manually using the binary method of Read & Nee (1995). Multi-male groups, terrestriality, polygamy, male dominance, and sexual dimorphism were compared with natal colouration and sexual dichromatism. The use of colouration data was unnecessary as both reflectance and brightness were treated as continuous variables. A summary of the results is shown in Tables 4.6 and 4.7, with a summary of the results from the test of independence and the comparative method using CAIC.

Some of the tests could not be performed because of the lack of contrasts made for variables throughout the order. When considering relationships with sexual dichromatism, polygamy generated only one contrast, and terrestriality, and male dominance none. Polygamy and terrestriality only generated one and two contrasts when compared with the occurrence of natal colouration, and could not be tested. Results show no significant correlation between sexual dichromatism and breeding system or sexual dimorphism, although sexual dichromatism was significantly correlated with natal colouration. Both breeding system and sexual dimorphism were not correlated with natal colouration. Clearly, the lack of evolutionary transitions in the relevant characters has seriously constrained some hypothesis testing.



Phylogenetic tree for the order Primates

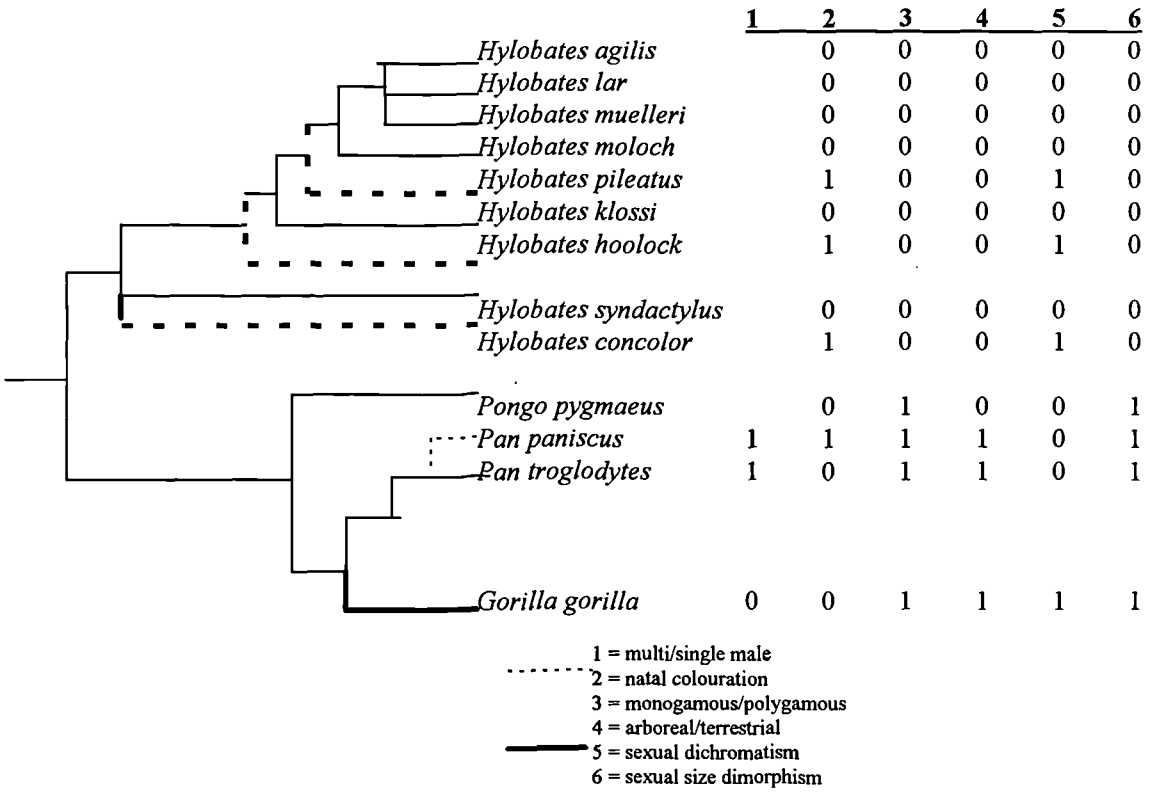


Fig. 4.4: The binary method of comparative analysis in the Hylobatidae and Pongidae

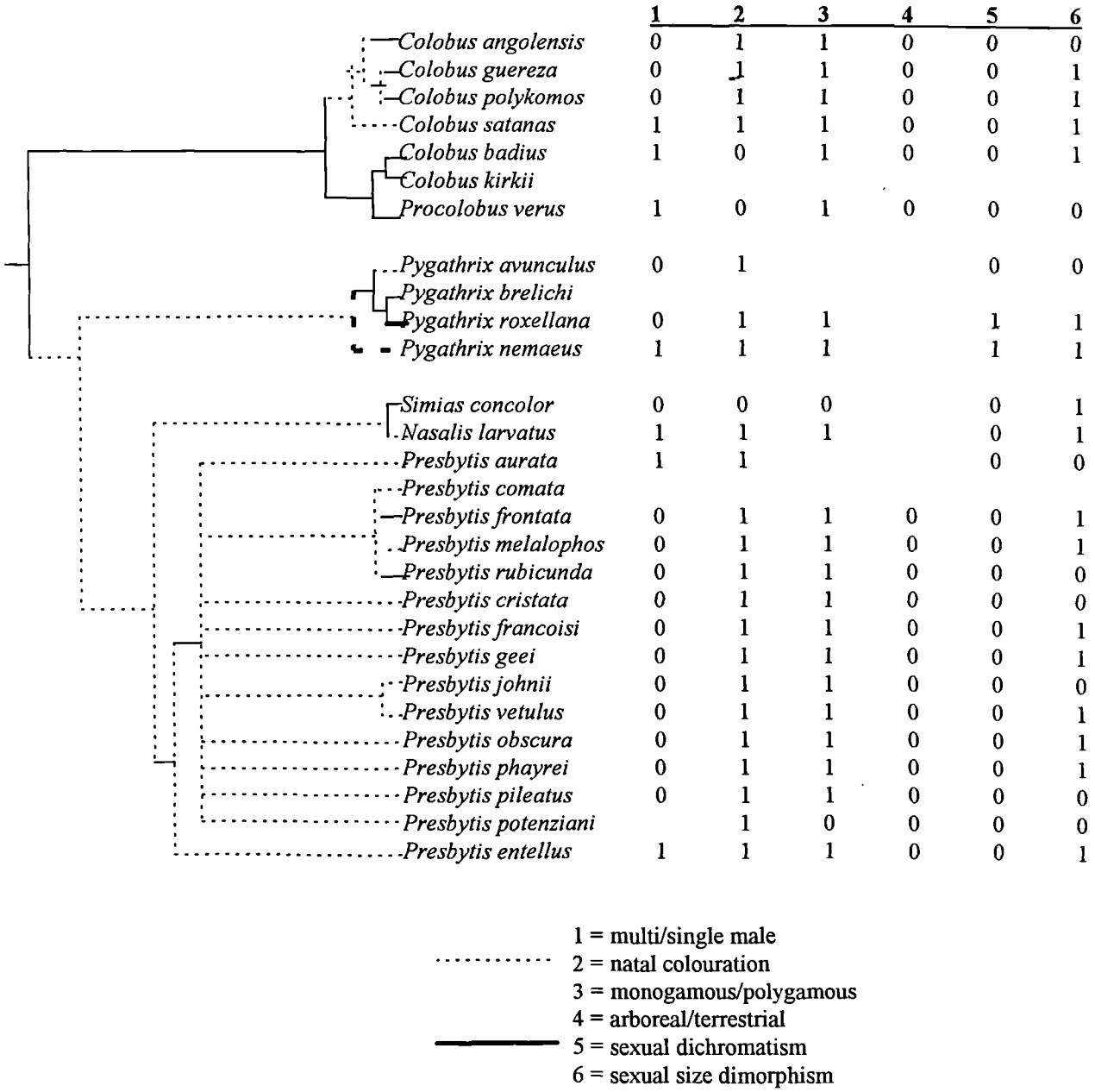
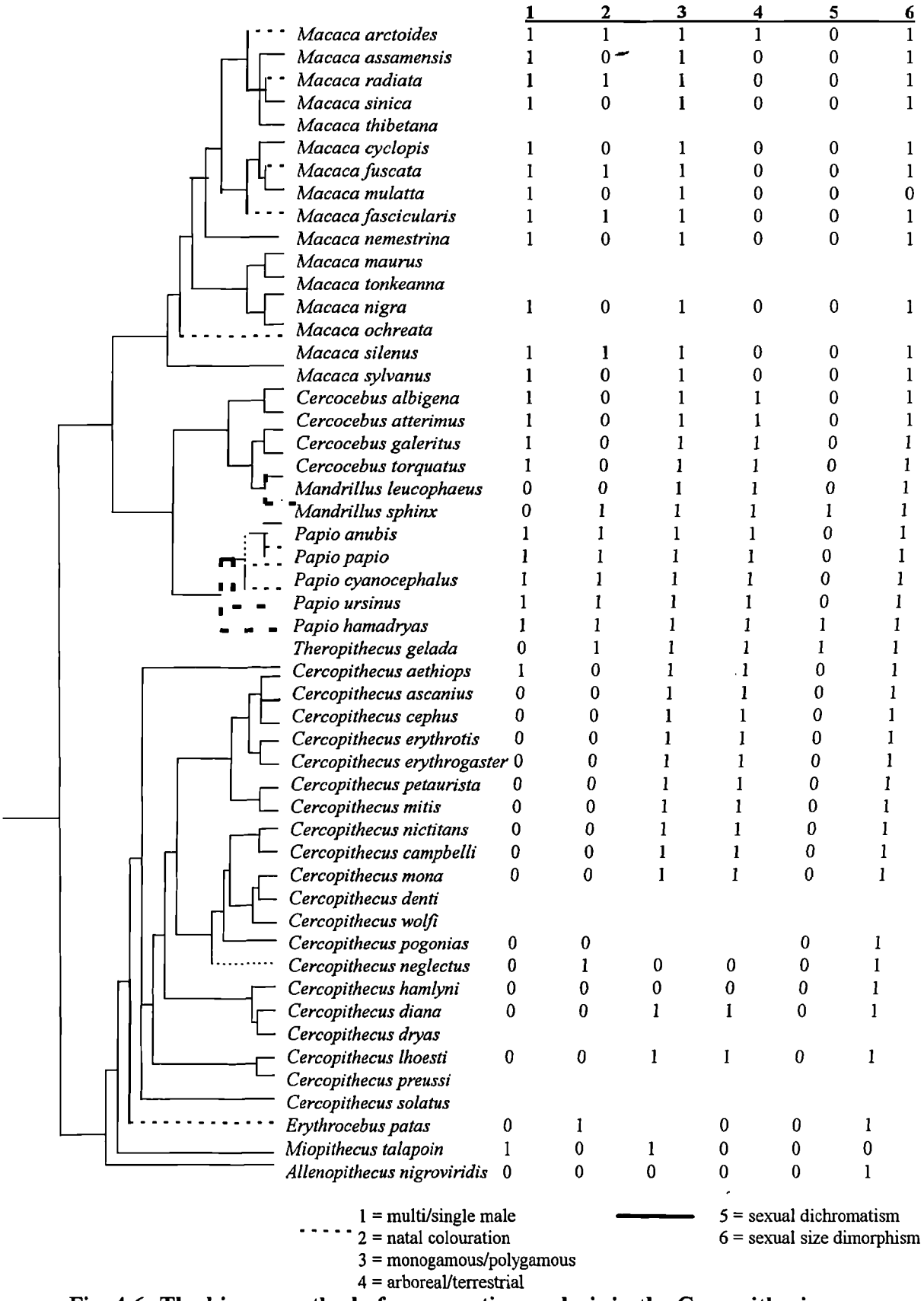


Fig. 4.5: The binary method of comparative analysis in the Colobinae



	1	2	3	4	5	6
Macaca arctoides	1	1	1	1	0	1
Macaca assamensis	1	0	1	0	0	1
Macaca radiata	1	1	1	0	0	1
Macaca sinica	1	0	1	0	0	1
Macaca thibetana						
Macaca cyclopis	1	0	1	0	0	1
Macaca fuscata	1	1	1	0	0	1
Macaca mulatta	1	0	1	0	0	0
Macaca fascicularis	1	1	1	0	0	1
Macaca nemestrina	1	0	1	0	0	1
Macaca maurus						
Macaca tonkeanna						
Macaca nigra	1	0	1	0	0	1
Macaca ochreata						
Macaca silenus	1	1	1	0	0	1
Macaca sylvanus	1	0	1	0	0	1
Cercocebus albigena	1	0	1	1	0	1
Cercocebus atterimus	1	0	1	1	0	1
Cercocebus galeritus	1	0	1	1	0	1
Cercocebus torquatus	1	0	1	1	0	1
Mandrillus leucophaeus	0	0	1	1	0	1
Mandrillus sphinx	0	1	1	1	1	1
Papio anubis	1	1	1	1	0	1
Papio papio	1	1	1	1	0	1
Papio cyanocephalus	1	1	1	1	0	1
Papio ursinus	1	1	1	1	0	1
Papio hamadryas	1	1	1	1	1	1
Theropithecus gelada	0	1	1	1	1	1
Cercopithecus aethiops	1	0	1	1	0	1
Cercopithecus ascanius	0	0	1	1	0	1
Cercopithecus cephus	0	0	1	1	0	1
Cercopithecus erythrotis	0	0	1	1	0	1
Cercopithecus erythrogaster	0	0	1	1	0	1
Cercopithecus petaurista	0	0	1	1	0	1
Cercopithecus mitis	0	0	1	1	0	1
Cercopithecus nictitans	0	0	1	1	0	1
Cercopithecus campbelli	0	0	1	1	0	1
Cercopithecus mona	0	0	1	1	0	1
Cercopithecus denti						
Cercopithecus wolfi						
Cercopithecus pogonias	0	0			0	1
Cercopithecus neglectus	0	1	0	0	0	1
Cercopithecus hamlyni	0	0	0	0	0	1
Cercopithecus diana	0	0	1	1	0	1
Cercopithecus dryas						
Cercopithecus lhoesti	0	0	1	1	0	1
Cercopithecus preussi						
Cercopithecus solatus						
Erythrocebus patas	0	1		0	0	1
Miopithecus talapoin	1	0	1	0	0	0
Allenopithecus nigroviridis	0	0	0	0	0	1

Fig. 4.6: The binary method of comparative analysis in the Cercopithecinae

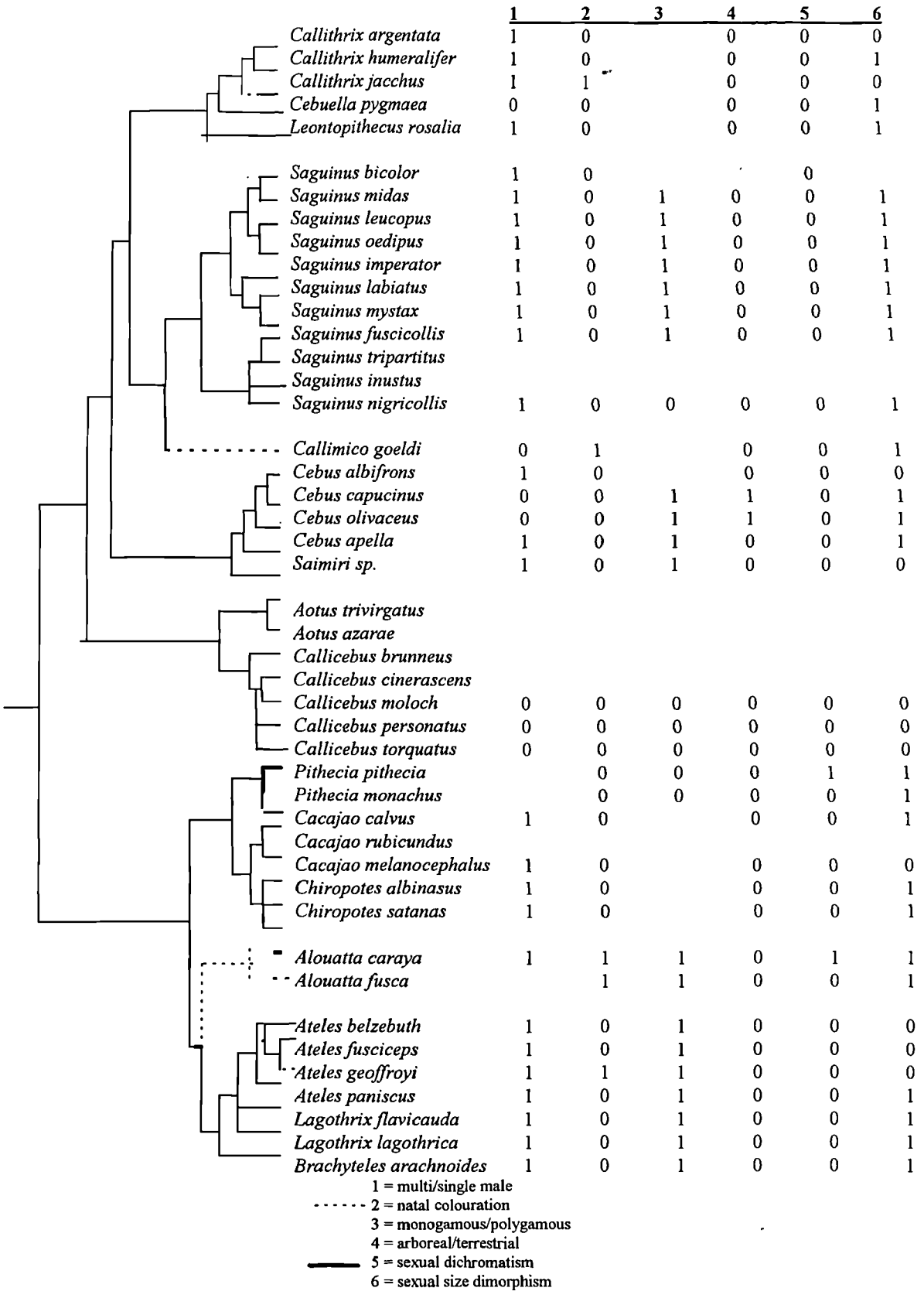
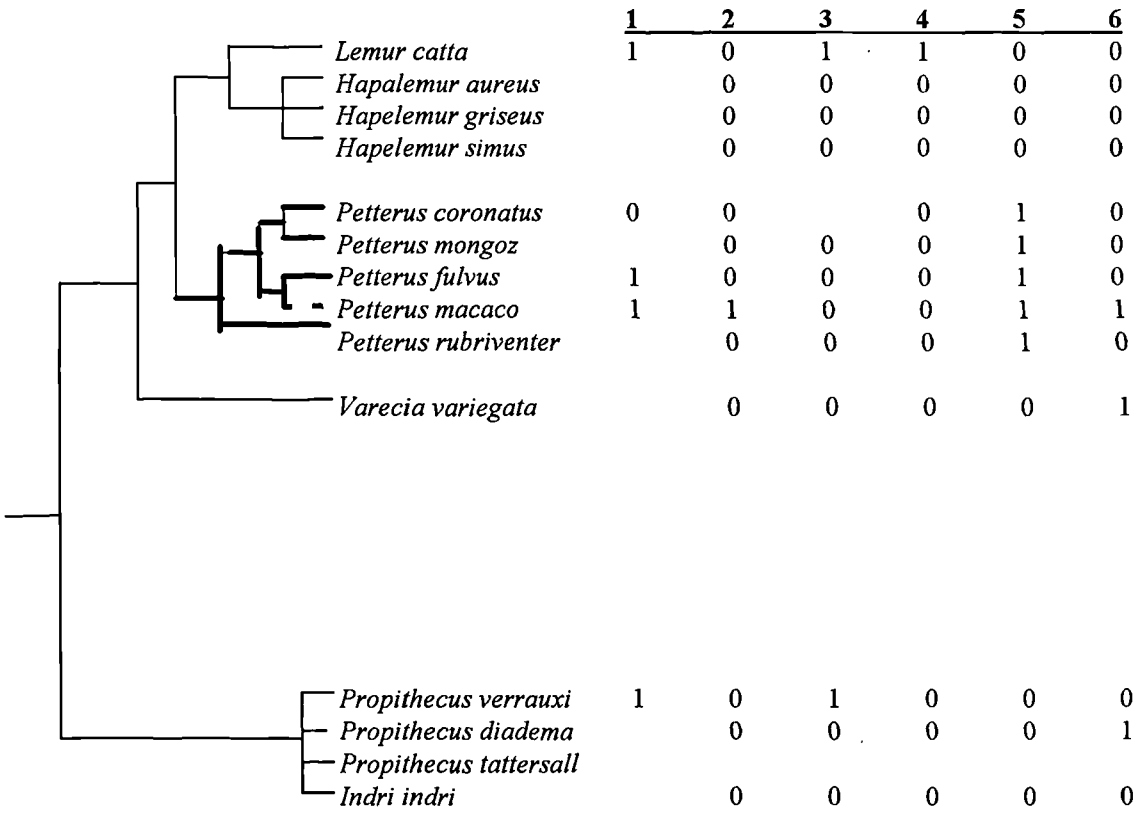


Fig. 4.7: The Binary method of comparative analysis in the Callitrichidae and Cebidae



..... 1 = multi/single male
2 = natal colouration
3 = monogamous/polygamous
4 = arboreal/terrestrial
5 = sexual dichromatism
6 = sexual size dimorphism

Fig. 4.8: The binary method of comparative analysis in the Strepsirhini

4.51 Comparative analysis and false-positives

The number of significant results which could occur by chance alone at a significance level of 5% was calculated for each comparative table. It was calculated that one significant result could be due to chance alone for each table, and thus act as a false-positive. The results are shown below in Table 4.61. The table illustrates that despite only one significant result being expected by chance alone, there are still more significant results than expected by chance. Despite being able to calculate the expected number of false-positives, it is impossible to discern which may have occurred by chance alone. Assurance and identification of real-positives can only be justified by a high *p*-value, or a trend in results. For example, males and females are significantly brighter in polygynous species (Table 4.3), and size dimorphism is significantly associated with or shows a trend with a high reflectance of female body parts (Table 4.4).

Table number	No. comparisons	No. significant		Expected significant	
		at 5%	at 10%	at 5%	
4.3	19	3	2	0.95	(1)
4.4	18	4	5	0.90	(1)
4.5	18	3	4	0.9	(1)
4.6	19	3	1	0.95	(1)

Table 4.61: Comparison of the number of expected false-positives with observed results

4.52 Confounding variables

As it was possible that some of the variables were not independent of each other, as assumed in the analysis, multiple regressions were performed to identify an association between the suspected variables. Table 4.62 highlights the results of the three multiple regressions performed on outputs from CAIC.

Variables		*p*	*t*
Male brightness vs.			
Regression coeff.:	Av. Group size	0.078	1.786
	Sexual size dimorphism	0.351	0.938
Anova:	the 2 independents	0.143	
Female brightness vs.			
Regression coeff.:	Av. Group size	0.044	2.046
	Sexual size dimorphism	0.237	0.813
Anova:	the 2 independents	0.128	
Natal brightness vs.			
Regression coeff.:	Av. Group size	0.836	0.207
	Sexual size dimorphism	0.848	0.192
Anova:	the 2 independents	0.962	

Table 4.62: Multiple regression outputs for pelage brightness

The multiple regressions for pelage brightness with average group size and sexual size dimorphism show that average group size is acting as a confounding variable with female brightness ($p = 0.044$), and possibly also with male brightness ($p = 0.078$), but not for natal brightness ($p = 0.836$). Sexual size dimorphism has no effect as a confounding variable in any of the three comparisons.

An additional comparative was performed to identify if average group size is significantly correlated with sexually size dimorphic species using the CRUNCH method in CAIC. However, there was no association ($p = 0.828$) confirming there is no relationship between size dimorphism and a species group size, but there is the confounding effect of average group size with pelage brightness (as described above). There were no significant results when pelage brightness was compared with average group size except for a trend with female pelage brightness, therefore it is assumed there is no real affect on the results, caused by group size acting as a confounding variable.

Further multiple regressions could not be performed using other suspected confounding variables such as mating system due to the dichotomous nature of the data. However, several comparisons were made in CAIC using BRUNCH for comparing a continuous and dichotomous variable. Group size and sexual size dimorphism was compared with mating system, and the outputs analysed using a *t*-test. There was no significant correlation between sexual size dimorphism and mating system ($p = 0.14$, $t = -1.59$). However, a trend was found between group size and mating system ($p = 0.07$, $t = 2.12$).

4.6 Summary of results

Comparative tests were performed in relation to functional hypotheses these are outlined in Table 4.11. The hypotheses are listed at the end of the chapter in relation to the results of this study (Table 4.10). Below the relationships are highlighted between the ecological, behavioural, and colouration characteristics.

1) In sexually dichromatic species infants tend to be brightly coloured, but males and females are not significantly brighter

2a) Male brightness is associated with diurnality

b) Both males and females are brighter in polygynous species

c) Females are more reflectant in sexually dimorphic species than non-dimorphic species

d) Females show a trend to be brighter in large groups

e) In male dominant species, males and females have a significantly more reflectant rump

f) Brightly coloured genitalia are associated with dull pelages in both males and females

g) Female ornamentation is associated with a dull chest and rump in males.

3a) Natal colouration is positively associated with both male and female brightness.

b) Natal colouration is positively associated with sexual dichromatism

4.61 Relationship between hypotheses and predictions

Eight functional hypotheses had predictions associated with the evolution of primate colourations. Each will be discussed separately and related to the predicted correlations in relation to the results.

The hypothesis that the evolution of sexual dichromatism is associated with sexual selection suggests several predictions, some of which are mentioned in the literature (refer to table 4.11). None of the predictions appear to be correlated with the evolution of sexual dichromatism, although there were insufficient contrasts to test male dominance. There was limited support for the evolution of a bright pelage due to sexual selection. The most striking is the correlation between polygamy and bright males and females. Rump reflectance was also significantly higher in male dominant species and lower in males with bright genitalia. Species with bright genitalia were also significantly duller for both males and females. There was a trend between bright females and group size and a significant association with sexual size dimorphism. Multi-male grouped species and sexually size dimorphic species do not seem to be associated with the evolution of a bright pelage in males. There is some support for the hypothesis that the evolution of pelage brightness must be associated with the visual system as both male and female adults are significantly brighter in species with a natal colouration. Males were also brighter in diurnal species. However, female brightness was not associated with diurnality. Another of the hypotheses suggested that pelage brightness could be associated with the habitat in which a species lives, with respect to the terrestriality or arboreality of a species. No correlation was shown between pelage brightness, sexual dichromatism or natal colouration with terrestriality. Female pelage brightness was not

correlated with female ornamentations, although bright males showed a trend with a less reflectant rump and a significantly less reflectant rump. One hypothesis suggesting the evolution of natal colouration could be associated with sexual selection showed no correlation with sexual size dimorphism and group size. Insufficient contrasts were available to perform the correlation between natal colouration and polygamous species. However sexual dichromatism significantly correlated with natal brightness and natal colouration. The final two hypotheses were based on the predictions of Treves (1997), where the evolution of a natal colouration could be correlated with the number of males in a group. Neither test showed any correlation with male grouping after accounting for phylogeny, despite multi-male system showing a significant correlation when compared using the two-way tables (refer to Table 4.2).

Hypothesis	Predictions		Tests (X= unable to test)
Evolution of sexual dichromatism is associated with sexual selection	Sexual dichromatism is associated with:	polygamy	Binary (X)
		sexual size dimorphism	Two-way table, Binary
		male dominance	Binary (X)
		multi-male grouping	Two-way table, Binary
		single male grouping	Two-way table, Binary (X)
		group size	CAIC
		bright males	CAIC
		bright females	CAIC
Evolution of a bright pelage is associated with sexual selection	Male/female pelage brightness associated with:	group size	CAIC
		sexual size dimorphism	CAIC
		polygamy	CAIC
		multi-male grouping	CAIC
		bright genitalia	CAIC
		male dominance	CAIC
Evolution of a bright pelage is associated with visual system	Diurnality is associated with:	bright males	CAIC
		bright females	CAIC
	Bright males and females are associated with:	natal colouration	CAIC
Evolution of a bright pelage is associated with habitat	Bright males and females are associated with:	terrestriality	CAIC
	Sexual dichromatism is associated with:	terrestriality	Binary (X)
	Natal colouration is associated with:	terrestriality	Binary (X)
Evolution of a bright pelage is associated with ornamentations	Bright males and females are associated with:	female ornamentation	CAIC
Evolution of natal colouration is associated with sexual selection	Natal colouration is associated with:	sexual size dimorphism	Two-way table, CAIC
		polygamy	Binary (X)
		group size	CAIC
		sexual dichromatism	Two-way table, Binary
Evolution of natal colouration is associated with infant defence	Natal colouration is associated with:	single male grouping	Two-way table, Binary (X)
Evolution of natal colouration is associated with the paternity	Natal colouration is associated with:	multi- male grouping	Two-way table, Binary

Table 4.7: Summary of the functional hypotheses, predictions and tests used

Sexual dichromatism is associated with:

a) *Test of Independence*

	Result
Sexual size dimorphism	NS
Multimale groups	NS
Natal colouration	NS

b) *CAIC*

	Result
Group size	NS
Size dimorphism (% weight)	NS
Bright males	NS
Bright females	NS
Reflectant males	NS (*for a dull chest)
Reflectant females	NS (*for a bright chest)
Natal brightness	+ (+ve)
Natal reflectance	NS

c) ***Binary Method***

	p	Result
Multimale groups	0.19	NS
Size dimorphism	0.56	NS

* $p \leq 0.05$
+ $p \leq 0.1$

Table 4.8: Summary of correlations with sexual dichromatism and pelage brightness using CAIC, the binary method and the test of independence

1a. Male pelage brightness (Using visual scale 1-3) is associated with:

CAIC	Result
Group size	NS
Sexual dimorphism	NS
Polygamy	* (+ve)
Terrestriality	NS
Diurnality	* (+ve)
Multimale groups	NS
Male dominance	NS
Female ornamentation	NS
Coloured genitalia	* (-ve)

1b. Male pelage reflectance is associated with:

CAIC	Result
Group size	NS
Sexual dimorphism	NS
Polygamy	NS
Terrestriality	NS
Diurnality	-
Multimale groups	NS
Male dominance	+ (Bright rump)
Female ornamentation	+ (Dull rump) * (Dull chest)
Coloured genitalia	+ (Dull rump)

2a. Female pelage brightness (Using visual scale 1-3) is associated with:

CAIC	Result
Group size	+ (+ve)
Sexual dimorphism	NS
Polygamy	* (+ve)
Terrestriality	NS
Diurnality	NS
Multimale groups	NS
Male dominance	NS
Female ornamentation	NS
Coloured genitalia	* (-ve)

2b. Female pelage reflectance is associated with:

CAIC	Result
Group size	NS
Sexual dimorphism	* (Bright pelage)
Polygamy	NS
Terrestriality	NS
Diurnality	-
Multimale groups	NS
Male dominance	+ (Bright rump)
Female ornamentation	_
Coloured genitalia	NS

* $p \leq 0.05$
+ $p \leq 0.1$
- = insufficient contrasts

Table 4.9: Summary of correlations with sexual dichromatism and pelage brightness using CAIC

Natal colouration is associated with:

a) ***Test of Independence***

	Result
Sexual dimorphism	NS
Multimale groups	*
Sexual dichromatism	NS

b) *CAIC*

	Result
Group size	NS
Sexual dimorphism	NS
Male brightness	* (+ve)
Female brightness	* (+ve)
Male reflectance	NS
Female reflectance	NS

c) ***Binary method***

	p	Result
Multimale groups	0.41	NS
Sexual dimorphism	0.73	NS
Sexual dichromatism	0.01	*

* $p \leq 0.05$
+ $p \leq 0.1$

Table 4.10: Summary of correlations with natal colouration and pelage brightness using CAIC, the binary method and the test of independence

A. Sexual dichromatism is associated with:	*Results*
1. Polygamous mating (Andersson, 1982)	Could not test
2. Sexual size dimorphism (Leutenegger & Chevereud, 1982)	No support
3. Multi-male groups (Wickler, 1967)	No support
4. Bright males (Darwin, 1871)	No support, dull chest
5. Dull females (Darwin, 1871)	No support, bright chest
6. Large group size	No support
7. Natal colouration (Darwin, 1871)	Support
B. Male pelage brightness is associated with:	
1. Diurnality (Jacobs, 1981)	Support
2. Sexual size dimorphism (Leutenegger & Chevereud, 1982)	No support
3. Sexual dichromatism (Darwin, 1871)	No, dull chest
4. Polygamy (Darwin, 1871)	Support
5. Terrestriality	No support
6. Female ornamentations	No, dull chest & rump
7. Multi-male groups (Andersson, 1994)	No support
8. Brightly coloured genitalia (Darwin, 1871)	No, dull pelage & rump
9. Male dominance (Wickler, 1967)	Partial support, bright rump
C. Female pelage brightness is associated with:	
1. Diurnality (Jacobs, 1981)	No support
2. No sexual size dimorphism or larger females	No support, more reflectant
3. Female ornaments (Darwin, 1871)	No support
4. Multi-male groups	No support
5. Polygamy (Irwin, 1994)	Support
6. Terrestriality	No support
7. Large groups	Partial support
8. No male dominance	No support, bright rump
D. Natal colouration is associated with:	
1. Sexual size dimorphism	No support
2. Multi-male groups (McKenna, 1981; Paul *et al.*, 1996; Treves, 1997)	No support
3. Single-male groups (Treves, 1997)	No support
4. Bright females (Darwin, 1871)	Support
5. Bright males (Darwin, 1871)	Support
6. Large group size (Alley, 1980; Treves, 1997)	No support
7. Sexual dichromatism (Darwin, 1871)	Support

Table 4.11: Summary of results in relation to the hypotheses

Chapter 5

Results (part two)

5.1 Testing the Hamilton-Zuk hypothesis in lemurs

Measurements of reflectance were made of individuals from two lemur species and analysed comparatively with parasite loads. Table 5.1 shows the raw results, including an individual's parasite counts and reflectance measurements. Appendix 3.1 lists 28 columns of raw data showing the species, the individual and their sex. For each individual, six columns show brightness measurements made using the spectrophotometer and are shown as percentage reflectance. Total reflectance is also displayed, which is the sum of all reflectance measurements for an individual. The remaining data columns involve information on an individual's parasite load obtained from faecal analysis. The faecal sample number is listed, and the number of worms is shown with reference to parasites *Strongyloides* (2 forms and sum total), and *Lemuricola* (refer to Figure 5.1). The average oocyte counts made from four fields of vision are displayed for the six parasite species in two forms; eggs per gram and average egg number. The parasite load of each individual was calculated as previously described using the sum of the mean total for each parasite species (App. 3.1). The mean total was obtained from a number of faecal samples varying by the number available during collection. Results also include the worm forms of the parasites found which were counted individually.

5.2 Reflectance variation between individuals

Table 5.1 shows the measurements taken from individuals of *Lemur catta* and *Eulemur fulvus rufus* to assess the brightness of each pelage and compare the intraspecific and interspecific variation in reflectance. The standard deviation of the total reflectance is more between males and females of *L. catta* than between the males and females of *E. f. rufus*, despite the latter displaying sexual dichromatism.

5.3 Parasites

One-tailed *t*-tests were performed to test the hypothesis that parasite loads are negatively associated with pelage colour brightness. The reflectance measurements of body parts (chest and crown) were compared with parasite load. These two body regions were selected as they are two areas that differ in colouration between the males and females of the sexually dichromatic species *E. f. rufus*. Five types of oocyte were present in the faecal samples and two types of worm; four of the species have been identified from Thienpont *et al.* (1986) and confirmed by the International Institute of Parasitology. Figure 5.2 is of the oocyte of *Strongyloides* sp., which was classed as (*s*), a medium-sized eliptical egg of 50-60 μm with a thin single wall containing a visible larva. Figures 5.3 and 5.4 are of fertilised and unfertilised oocytes of *Ascaris lumbricoides*, classed as (*t*) and (*f*); the total *A. lumbricoides* infection is labelled (*asc*). *Ascaris* oocytes are medium in size (45-75 μm), golden brown and usually three-layered with a thick outer wall, a thick middle layer and an inner layer containing a thin

yolk membrane. The distinction between fertilised and unfertilised oocytes can be made by the presence of a thick albuminous outer wall (Thienpont-*et al.*, 1986). Figure 5.5 is of an unidentified oocyte (*d*). The large spherical oocyte (Figure 5.6) is parasite (*h*), which is possibly *Fasciola hepatica* as the eggs are large and elliptical with a thin outer wall and granular contents. Figure 5.7 is the unidentified parasite (*k*), possibly *Enterobius vermicularis* which is an ovoid medium sized egg (35-45μm), with 4 layers containing a larva.

Name	Sex	D.O.B.	Site	Total reflectance (%)	$\bar{\chi}$	σ
Lemur catta						
Lycus	m	'85	NHE-4	186		
Charops	m	'94	NHE-4	164		
Valgius	m	'95	NHE-4	165		
Aracus	m	'91	NHE-4	208		
Philocles	m	'92	NHE-4	144		
Agnostes	m	'87	NHE-4	210		
Cercops	m	'95	NHE-4	187	180.57	24.30
Dory	f	'89	NHE-4	179		
Alice	f	'89	NHE-4	172		
Thyrea	f	'93	NHE-4	163		
Charissa	f	'94	NHE-4	145		
Cassandra	f	'94	NHE-4	203		
Cleis	f	'85	NHE-4	177	173.17	19.17
				Total σ		20.67
Eulemur fulvus rufus						
Carmine	m	'92	NHE-4	97		
Rory	m	'89	NHE-2	52		
Redoak	m	'93	NHE-2	85		
Sorrel	m	'80	NHE-2	58	73.00	21.49
Rosella	f	'92	NHE-2	77		
Redbay	f	'95	NHE-2	55		
Redwood	f	'94	NHE-4	72		
Strawberry	f	'94	NHE-4	92		
Redlake	f	'83	NHE-4	89	77.00	14.80
				Total σ		16.95

$\bar{\chi}$ = mean reflectance
σ = standard deviation

Table 5.1: Intra- and interspecific comparisons of pelage reflectance

5.4 Correlations between pelage reflectance and oocyte load

Table 5.2 shows the oocyte parasite load for each species found in the lemurs. The results are divided into males and females for each species, to identify any correlation between an individual's sex and their parasite loads. Results are shown for the six parasite species (Table 5.2). Results are indicated by the p and t-values from a one-tailed t-test and their significance ($p < 0.05$) summarised. Parasite *d* was the least commonly found parasite and there were no results for males in *E. f. rufus* and females in *L. catta*. In total there were three significant correlations identified (and two suggestive results), between overall pelage brightness and a low parasite load. There were no significant correlations for *E. f. rufus* males or *L. catta* males. *E. f. rufus* females showed significant correlations between brightness and parasites *e* and *k*. *L. catta* females showed the same relationship for parasite *h*. When the results for female and male *L. catta* were combined, parasite and *A. lumbricoides* showed significant results (Table 5.2).

A second comparative analysis was performed considering the reflectance of particular body areas, the chest and the crown separately. These two body parts are commonly different in sexually dichromatic species or brighter in monochromatic species. There were a few significant results where a higher pelage reflectance in the crown or chest region correlated with oocyte load (Table 5.3). Male *E. f. rufus* showed no significant correlations, only a trend with the chest region and parasite (*h*). Female *E. f. rufus* had no correlations with oocyte load. Female *L. catta* showed a trend for the chest brightness correlating with low

levels of *Lemuricola* ($p = 0.08$). Male *L. catta* showed a trend with *Ascaris* oocytes ($p = 0.6$) for chest brightness and a significant correlation for parasite (k) for both crown and chest regions.

5.5 Correlations between *Lemuricola* worm load and pelage reflectance

Table 5.4 shows the results for the correlation of average *Lemuricola* worm load with chest and crown reflectance. There were no significant correlations for males in *E. f. rufus*, but female crowns were significantly correlated with a high worm load. In females, the crowns are cream/grey; in males, they are brown/ginger. In *L. catta* males, the crown showed a trend to correlate with *Lemuricola* worm load ($p = 0.1$), but with females, there was no correlation. The results are summarised in relation to the hypotheses in Table 5.5.

5.6 Parasite loads of wild and captive lemurs

The parasite loads were also calculated for wild *L. catta* individuals using faecal samples collected from Madagascar and for *Eulemur macaco* and *Varecia varecia* from faecal samples collected from London Zoo (App. 3.2). The wild and captive species are used as a control for the free-ranging lemurs at DUPC. The individual, sex and sample numbers are shown. Only one sample was collected per individual. Four counts were conducted in the same manner as for the semi-wild lemurs at DUPC. No parasites were found in the two

individuals at London Zoo despite the animals never being wormed. The wild lemurs were only infected with *A. lumbricoides*; two of the individuals had a stool with the worm form. Low levels of the oocyte were found in fertilised and unfertilised forms in the majority of the Wild lemurs, with the exception of the only infant, and one male and female from the Yellow group.

5.7 Comparative analysis and false-positives

The number of significant results which could occur by chance alone at a significance level of 5% was calculated for the three comparative tables, same method as in Chapter 4, 4.51. It was calculated that for Tables 5.2 and 5.3, up to two significant results could be due to chance alone, and up to one significant result in Table 5.4. These results will be false-positive results due to chance, and the number of comparisons made in each table. The results are shown below in Table 5.11. However, as for the results in Chapter 4, the number of expected significant false-positives is less than the number of observed significant correlations indicating that the majority of results can still be accepted as true.

Table number	No. comparisons	No. significant		Expected significant	
		at 5%	at 10%	at 5%	
5.2	29	4	1	1.45	(1-2)
5.3	42	3	3	2.1	(2)
5.4	8	2	0	0.4	(0-1)

Table 5.11: Comparison of the number of expected false-positives with observed results

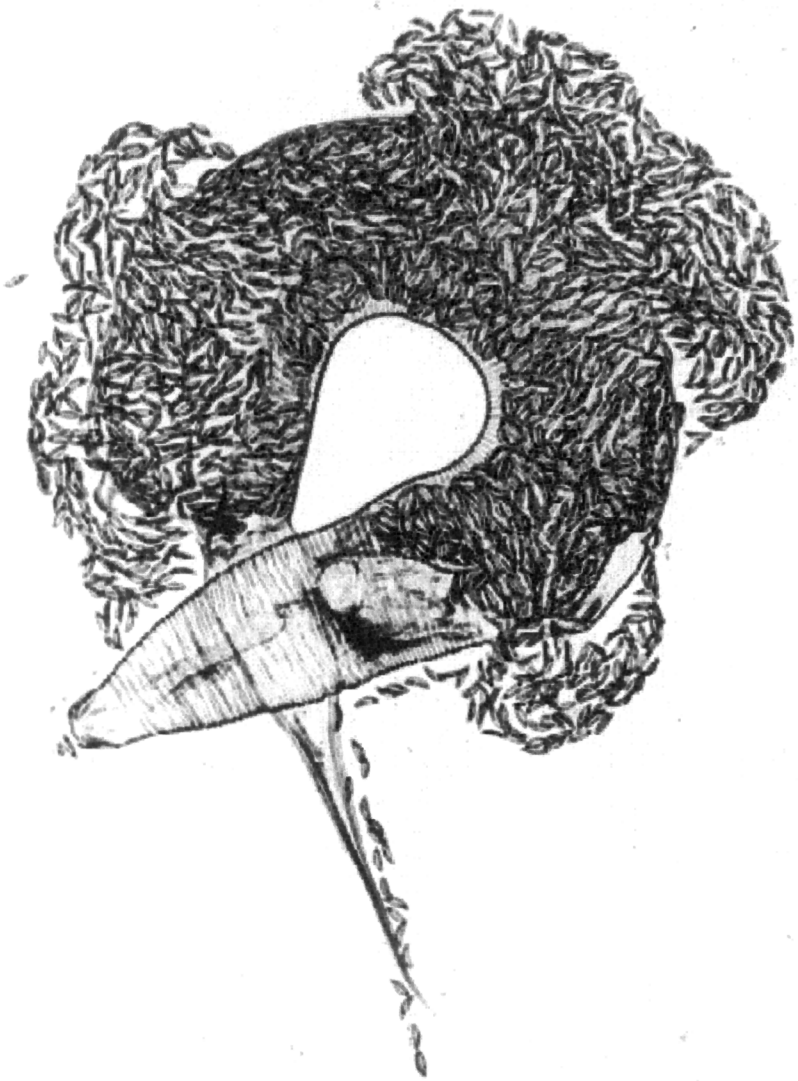


Figure 5.1: Gravid female worm of *Lemuricola* sp. containing oocytes (mag. x40).

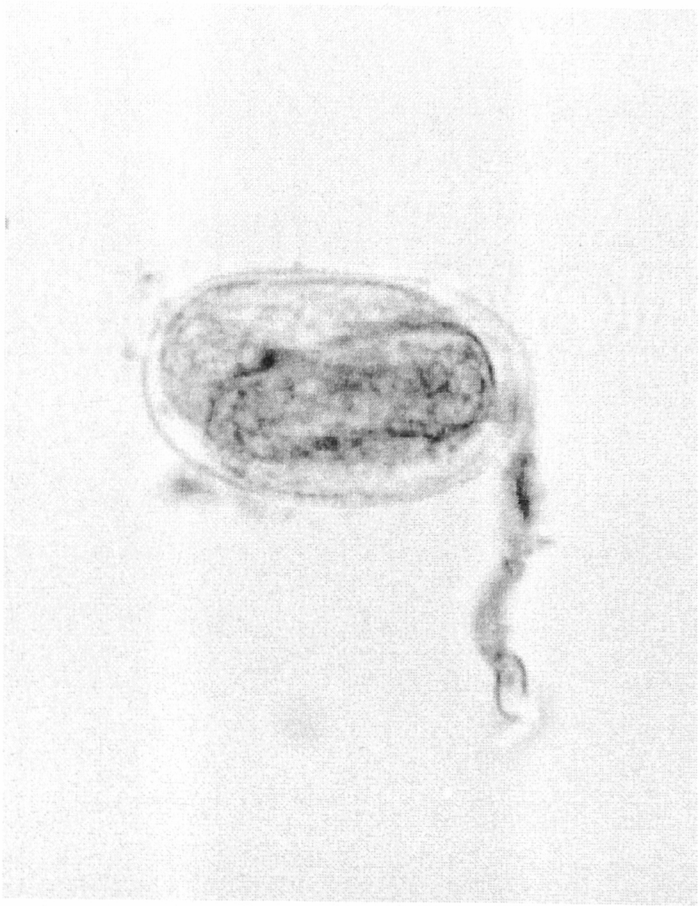


Figure 5.2: Oocyte of Strongyloides sp. coded as (s) (mag. x250)

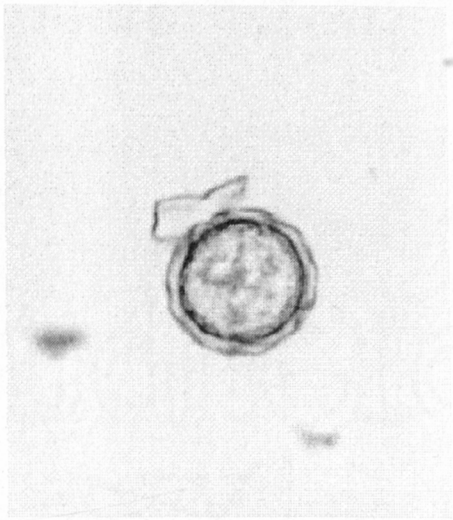


Figure 5.3: Fertilised oocyte of *Ascaris lumbricoides*, coded as (t) (mag. x250).

Figure 5.4: Unfertilised oocyte of *Ascaris lumbricoides*, coded as (f) (mag. x250)

Figure 5.5: Unidentified oocyte, coded as (h) (mag. x250).

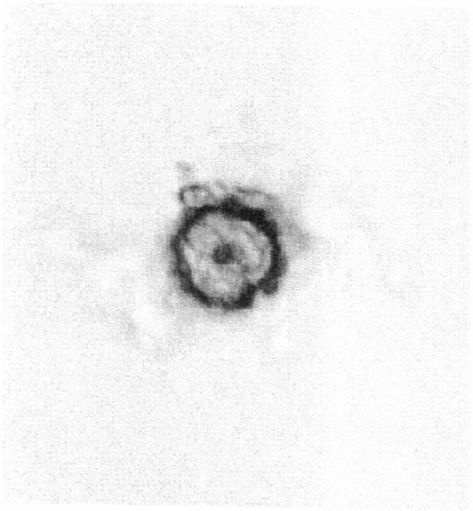


Figure 5.6: Unidentified oocyte, coded as (d) (mag x250).

Species	Parasite	*p*	*t*	Significance
male *L. fulvus rufus*	e	.20	-.26	NS
	h	.29	.63	NS
	asc	.27	.76	NS
	k	.34	.57	NS
	d			
	s	.19	1.11	NS
female *L. fulvus rufus*	e	.03	-2.86	*
	h	.39	.30	NS
	asc	.42	.22	NS
	k	.03	-2.84	*
	d	.22	.88	NS
	s	.17	1.01	NS
male *L. catta*	e	.24	.75	NS
	h	.20	-.92	NS
	asc	.48	-.07	NS
	k	.36	-.37	NS
	d	.27	-.66	NS
	s	.24	.75	NS
female *L. catta*	e	.36	.39	NS
	h	.04	-2.33	*
	asc	.36	.36	NS
	k	.31	-.54	NS
	d			
	s	.48	.05	NS
all *L. catta*	e	.40	-.26	NS
	h	.05	-1.66	*
	asc	.06	-1.69	+
	k	.38	-.33	NS
	d	.29	-.57	NS
	s	.41	.23	NS

$^{+}$ $p \leq 0.1$; * $p \leq 0.05$; one-tailed *t*-test
p = *p*-value
t = *t*-value
Parasite oocytes: asc=*Ascaris lumbricoides* (Fig. 5.3 and 5.4)
e = *Lemuricola* sp.(Fig.. 5.1)
s = *Strongyloides* sp.(Fig. 5.2)
h = unidentified (Fig. 5.5)
k = unidentified (Fig. 5.7)
d = unidentified (Fig. 5.6)

Table 5.2: Correlations of oocyte parasite load with mean pelage reflectance

Species	Parasite	Body part	*p*	*t*	Significance
male *L. fulvus*	*e*	cr	.25	.81	NS
		ch	.26	1.30	NS
	h	cr	.43	.21	NS
		ch	.01	6.53	*
	asc	cr	.36	-.43	NS
		ch	.43	-.20	NS
	k	cr	.24	.87	NS
		ch	.18	1.14	NS
female *L. fulvus*	*e*	cr	.27	-.67	NS
		ch	.08	-1.81	+
	h	cr	.47	.067	NS
		ch	.19	-1.05	NS
	asc	cr	.18	1.38	NS
		ch	.46	-.13	NS
	k	cr	.37	-.34	NS
		ch	.34	-.46	NS
female *L. catta*	*e*	cr	.14	-1.25	NS
		ch	.11	1.50	NS
	h	cr	.41	.25	NS
		ch	.12	-1.37	NS
	asc	cr	.48	.05	NS
		ch	.08	-1.68	+
	k	cr	.20	.95	NS
		ch	.17	-1.09	NS
male *L. catta*	*e*	cr	.42	-.20	NS
		ch	.47	.08	NS
	h	cr	.19	.97	NS
		ch	.31	.53	NS
	asc	cr	.06	1.83	+
		ch	.46	.11	NS
	k	cr	.01	3.47	*
		ch	.20	-.94	NS
	d	cr	.01	3.24	*
		ch	.17	-1.05	NS

$^{+}$ $p \leq 0.1$; * $p \leq 0.05$; one-tailed *t*-test
p = *p*-value
t = *t*-value
cr = crown reflectance
ch = chest reflectance

Parasite oocytes: asc = *Ascaris lumbricoides* (Fig. 5.3 and 5.4)
e = *Lemuricola* sp.(Fig.. 5.1)
s = *Strongyloides* sp.(Fig. 5.2)
h = unidentified (Fig. 5.5)
k = unidentified (Fig. 5.7)
d = unidentified (Fig. 5.6)

Table 5.3: Correlations of mean parasite loads with chest and crown reflectance

Species	Body part	*p*	*t*	Significance
male *L. fulvus*	crown	.18	1.15	NS
	chest	.18	-1.15	NS
female *L. fulvus*	crown	.04	-2.77	*
	chest	.42	.22	NS
male *L. catta*	crown	.01	3.24	*
	chest	.17	-1.05	NS
female *L. catta*	crown	.20	.94	NS
	chest	.17	-1.09	NS

$^{+}p \leq 0.1$; * $p \leq 0.05$; one-tailed *t*-test

Table 5.4: Correlations of *Lemuricola* sp. worm loads with crown and chest reflectance

Hypotheses

1. Pelage reflectance varies between individuals but is greater between species
   Result: not in captive lemurs

2. Pelage reflectance varies more between sexes in dichromatic species
   Result: reject hypothesis

3. Parasite load is negatively associated with pelage reflectance
   Result: Oocyte loads provide only very limited support

4. Parasite load is negatively associated with the reflectance of the chest and crown regions
   Result: partial support for this hypothesis with reference to *Lemuricola* sp. worms and oocyte loads

5. Sexually dichromatic species are susceptible to a greater number of parasites
   Result: reject hypothesis

6. Parasites found in free-ranging captive lemurs do not differ from wild lemurs, but do differ from captive-bred lemurs
   Result: partial support

Table 5.5: Summary of Significant results

Chapter 6

Discussion

6.1 Pelage colour and communication

The aim of the study was to identify evolutionary correlates of pelage colouration brightness and ornamentation. Two forms of "badge" that are used to communicate a message have been described (Smith, 1980); the first provides a sustained background of information about the communicator. The second identifies and provides information on behaviour patterns that are communicated by the "badge". Each must be adjustable over time and have more than one state, the duration of which is dependent on the nature of the information (Smith, 1980). Intraspecific pelage colouration fits the second category of "badge", where the development of sexual dichromatism occurs at sexual maturity, and pelage brightness, and size of ornament varies between individuals. A natal pelage is present from birth, through the period of early dependency, until the developmental stage when an infant can identify and locate its mother (Swartz and Rosenblum, 1981). In both cases, the method of communication is known, often using a brighter pelage and ornamentations, but the interpretation of the signal is disputed. Characteristics that may be associated with the evolution of pelage colour will now be discussed.

The research was divided into two parts, interspecific comparative analysis and intraspecific comparisons using fieldwork. The pelage colouration of an individual, or a species, can signal a wealth of information about the individual. In the case of natal colouration, the communicator, a primate infant, is signalling its age to elicit a response from the conspecifics. The young age of the infant may indicate the needs, and status of the infant, signalling vulnerability, dependency on others, and sub-ordinance. Natal colouration may elicit a range of responses including interest, protection, suppressed aggression and maternal behaviour. When pelage colour is used to communicate sex

differences in adult primates, the form of communication is the same but the signals are entirely different from a natal pelage. A sexually dichromatic pelage can signal dominance, strength, health, genetic fitness, parental abilities may serve to endear a prospective partner, or to enhance the individual's competitive ability over conspecifics.

6.2 Distribution of intraspecific pelage colourations across the order

The distribution of natal colouration and sexual dichromatism across the primates shows how both forms of visual communication have evolved in the order. The most important and immediately obvious feature of the distribution of intraspecific pelage variation is that no nocturnal species display either a natal or a sexual pelage. The dichromatic or trichromatic visual system of diurnal primates is redundant in the nocturnal environment when colour cannot be visualised. Therefore, most nocturnal primates have a pure rod retina (Jacobs, 1981). The conclusion drawn from the fact that the 26 nocturnal primates do not display intraspecific pelage variation is that colour is used as a visual form of communication in diurnal primates. Nocturnal species however, can visualise patterns between tones of grey, black and white. The reason for not using pelage patterning instead of colour to distinguish between individuals either sexually or ontogenetically remains unanswered, but could be associated with a need to be cryptic. It does suggest that the signal is about quality of individuals, rather than identity.

Sexual dichromatism is present in both the Strepsirhini and the Haplorhini (Table 3.1). Five of the twelve diurnal strepsirhines (all of which are true lemurs) have sexual dichromatism. *Eulemur macaco*, the black lemur is named after the male, which has a

black, silky pelage. The females are a rusty red with a white ventral pelage and white ear tufts (Wolfe and Sleeper, 1997). Although the male is black, it is more noticeable than the female pelage. *E. rubriventer*, the red-bellied lemur, has a red ventral pelage, and the males and females differ is face colouration; the males are more red and have red cheek whiskers, where females have white whiskers (Napier and Napier, 1985). *E. mongoz*, the mongoose lemur, and *E. coronatus*, the crowned lemur, also display sexual dichromatism. The mongoose lemur male has a red neck, head and cheeks compared to the whiter, greyer female (Tattersall, 1982). Crowned lemur females are lighter with a grey pelage and pale cheeks, compared to the darker brown pelage of the male (Wolfe and Sleeper, 1997). In *E. f. rufus*, one of the subjects in the field study, the female is visually "brighter" with a red/chestnut pelage and white/grey crown, the males are uniformly grey with a chestnut/brown crown. Lemurs are not strictly diurnal and some are described as cathemeral, as they are most active at dawn and dusk, sleeping through the middle of the day. It is surprising that species that are not strictly diurnal and have dichromatic vision use pelage colour as a means of signalling sex differences. There appears to be no reason for only *Eulemur* to display sexual dichromatism, and not other lemuroids such as the indri, or *Lemur catta*, the ring-tailed lemur. Sexual dichromatism is relatively evenly distributed in the platyrrhines and the catarrhines at 5% and 11% respectively. The hominoids have a higher percentage of sexually dichromatic species at 31%. This is due to the gibbons, of which three species are dichromatic. Fourteen percent of all diurnal primates display sexual dichromatism. This figure does not include other secondary sexual characteristics such as bright genitalia and ornaments.

Only one strepsirhine displays a natal pelage, *Eulemur macaco*, the black lemur has dark grey infants that are similar to, but lighter than, the adult male pelage. In the other true

lemurs, the infants are similar in colour to the female adult pelage. Only ten percent of the platyrrhines display a natal colouration, compared to 54 % for cercopithecoids and hominoids. Thirty-six Old World monkey species display a natal pelage, compared to only seven species that display a sexually dichromatic pelage. The reason so many cercopithecoids display a natal pelage is due to the langurs (14 species), all of which have vividly coloured natal coats. The langurs are a good example of closely related species sharing a characteristic by common descent. In total, 37% of diurnal primates display a natal colouration. There are a number of possible ecological or behavioural reasons for this distribution across the primates, such as energetic costs, predation risks and female choice.

6.3 Why use three comparative methods?

The use of two-way tables, which do not account for closely related character similarities, illustrates the need for phylogenetic adjustment before statistical analysis. Although only seven of the many hypotheses to be further tested using CAIC and the binary method were analysed using the test of independence; these were sufficient to illustrate two major points. The first is that the inclusion of nocturnal species in comparative tests swamps relationships with other variables as there are no nocturnal species that display intraspecific pelage variation. Significant results differed when testing the association between natal colouration and sexual size dimorphism. With the exclusion of the 26 nocturnal species, the two were no longer correlated. As already mentioned none of the nocturnal species display a natal colouration, yet the inclusion of the nocturnal species in the two-way table is sufficient to bias the results and disguise true

correlations. Also when the nocturnal species were omitted from the test, natal colouration was found to significantly correlate with a multi-male mating system, when it was not significant with nocturnal species. The second important point for the need to control for phylogenetic non-independence will be illustrated later. The results of the two-way tables and the test of independence were then compared with results from CAIC (Purvis and Rambaut, 1995) and the binary method (Read and Nee, 1995).

6.4 Interpretation of CAIC Results

6.41 Pelage brightness and ecological correlations with sexual dichromatism

The first part of the CAIC analysis was to determine ecological and behavioural correlations with sexual dichromatism and the pelage colour brightness of each sex (Table 4.3). Nineteen comparisons were performed between ecological correlates, sexual dichromatism and pelage brightness, of which five had statistical significance. The results suggest that the evolution of sexual dichromatism is not associated with sexual size dimorphism, or group size. Sexual size dimorphism and sexual dichromatism are both described as secondary sexual characteristics (Darwin, 1871). However, the lack of a correlation indicates that dichromatism should be linked to intersexual selection (mate choice) and sexual size dimorphism to intrasexual selection. The mechanisms selecting for the two must be different. There was no correlation between sexual dichromatism and large group size. Large group size was considered to have an association with sexual dichromatism due to an increase in competition for mates within the group. This of course, would also be dependent on the number of males in the group and the mating system practised, all of which could mask the influence of a large group size on the

evolution of sexual dichromatism.

A surprising result is that neither male nor female brightness correlated with the presence of sexual dichromatism. It would be expected that males are most often brighter in sexually dichromatic species. There are very few exceptions in primates where the female is brighter for example, *Eulemur fulvus rufus*. If brighter females in sexually dichromatic species had an effect on the evolution of sexual dichromatism, it would be expected that both males and females would be bright. This result however, does not disprove Darwin's observation that in most sexually dichromatic primate species, the male is brighter. The bright and vivid use of colour throughout the primates, by those that are not dichromatic, could mask correlations between pelage brightness and sexual dichromatism. Natal pelage brightness did show a trend of correlation with sexual dichromatism, indicating that sexually dichromatic species have bright infants. If this trend indicates an association between sexual dichromatism and natal colouration, the correlation is puzzling, because in sexually dichromatic species the infant most often resembles the duller female. Perhaps it reflects a relaxation pressure, where all individuals can use bright visual signals.

There were two significant results when the ecological and behavioural traits were compared with male pelage brightness. Polygamy and diurnality were both significantly correlated with bright males. Diurnality would be expected to have an association with bright males for the reasons previously discussed concerning colour vision. It is interesting to note that diurnal females were not brighter. Polygamy is also significantly correlated with bright males and females. This indicates that polygamous species generally have brighter pelages. Unfortunately, there were insufficient contrasts between

polygamy and sexual dichromatism to identify any correlation using the binary method. It must therefore be assumed that polygamous species are brighter. This is probably due to mate choice for a bright pelage that is inherited equally through both sexes (Darwin, 1871). Mating system, terrestriality, and male dominance had no association with the brightness of a male or female pelage.

6.42 Pelage reflectance and sexual dichromatism

Fourteen comparisons were made between sexual dichromatism, ecological and behavioural variables, and male and female pelage reflectance. The chest region showed a correlation with sexual dichromatism in both males and females. The correlation however, did not give the same result, as males have a duller chest and females a more reflectant (lighter) chest in sexually dichromatic species. This could be associated with colour saturation in males, as they are often darker than females in sexually dichromatic species; for example *Eulemur macaco* and *Hylobates concolor* (see Appendix 1.8). Only one trend was identified between male reflectance and the ecological and behavioural variables, that of male dominance. The comparison showed a non-significant trend for species that are male dominant to have a highly reflectant rump. This result may be involved with dominance signalling, similar to the silver back of dominant male gorillas. It is interesting to note that females also show a trend between rump reflectance and male dominance, but female rumps are duller and less reflectant in male dominant species. Another variable, which correlates with the reflectance of a female's rump, is the presence of extreme sexual size dimorphism. The rump correlated so strongly ($p < 0.0001$) with size dimorphism, that the reflectance of the other five body parts were also

included in the comparison. The crown, cheek, back and outer leg regions showed a trend to be duller in size dimorphic species. The mean pelage reflectance was also calculated from all body parts, and showed a significant correlation with size dimorphism. The results of this comparison show that, without doubt, the female pelage is significantly less reflectant in size dimorphic species (when the female is less than 90% of the male body weight). This could be attributable to habitat where size dimorphic species are generally terrestrial with a greater need for a cryptic colouration. The relationship between sexual size dimorphism and dominance has previously been discussed (Andersson, 1994; Harcourt and Stewart, 1987). The less reflectant rump (and possibly pelage), could be a signal of sub-ordinance, as suggested by previous comparisons. Male rump reflectance is not significantly correlated with size dimorphism. It is possible that male dominance is being signalled using body size; therefore female ranking requires another form of signalling dominance such as rump reflectance. To consider an alternative theory, it has been suggested that males are larger due to competition for females (Andersson, 1994), and could select the "best" females using rump reflectance as an index of fitness. The more reflectant the rump, the "fitter" the female. This hypothesis could also be linked to the Hamilton-Zuk hypothesis where pelage reflectance is associated with the health or genetic fitness of the individual (Hamilton and Zuk, 1983). Female rump reflectance also shows a trend with mating system. This result could also be associated with fitness and mate choice. The female rump is most reflectant in multi-male grouped species. Rump brightness could be used as an index of fitness for females, or as a signal of individual female hierarchy. Many primates show oestral reddening of the buttocks and surrounding rump; rump brightness could be an extension of this "fertility" signal. The pelage brightness of the hair surrounding the buttocks could act as a permanent signal, unlike the reddening

associated with a readiness to mate.

6.43 Pelage brightness and reflectance correlations with ornamentations and bright genitalia

Pelage brightness, sexual size dimorphism and group size had no correlation with the presence of ornamentations in females. Male mean pelage reflectance did not correlate with female ornamentations, and there were insufficient contrasts to statistically compare with female mean reflectance. The chest region of males appears to be consistently less reflectant, due to a darker appearance. It is possible that rump reflectance is used in signalling information about the individual, such as status or health.

Species with bright genitalia are duller, in both males and females. Both sexes show a significant negative correlation between bright genitalia and pelage brightness. Bright genitalia must be used as a form of sexual signalling, which is known to be commonly frontal (Andersson, 1994). A good example of bright genitalia being hidden or highlighted by a dull pelage, until displayed, is *Cercopithecus aethiops*, the vervet monkey. It is a cryptic silver-grey in both males and females, yet males have a white perineal skin, and a scarlet penis surrounded by a blue scrotum. This could not be described as anything but a secondary sexual characteristic. The multi-male grouping of *C. aethiops* requires the formation of a dominance hierarchy. Males display by holding their tail erect, giving a red, white and blue display to assert their dominance (Napier and Napier, 1985). The use of bright genitalia in *C. aethiops* must be sexually selected, through female choice or by male competition for a mate. To give further support for the

signalling of dominance, the only other significant correlation with bright genitalia was the trend for a dull rump in males. The dull rump could be used to create as much contrast as possible to accentuate the bright genitalia; it may also be used in signalling dominance. There were no significant correlations with sexual size dimorphism, or large group sizes and bright genitalia, possibly suggesting that female choice could be the result of bright genitalia, rather than sperm competition.

6.44 Correlations between natal colouration and brightness, ecological and behavioural variables

Unlike sexually dichromatic species, in species with natal coats the adults are commonly bright. This result may relate to the hypothesis proposed by Hrdy (1970) to be linked with a relaxation in predation pressure; the less the risk from predation, the brighter the pelage. This may also apply to the adults. Results however, show no association between terrestriality and natal brightness, bright adults or the presence of sexual dichromatism. It has also been demonstrated that there is no correlation between a relaxation in predation pressure and the presence of a natal pelage (Ross and Regan, in press). The reflectance of a natal pelage does not correspond to the brightness of the pelage, as there is no correlation between a natal pelage and pelage reflectance. A bright natal pelage does show a trend with the presence of sexual dichromatism in a species. The mechanism may be unrelated, or could suggest that natal colouration correlates with the presence of sexual dichromatism (see below).

To consider the second set of comparisons involving bright genitalia and female

ornaments, one comparison between ornamentation and natal mean reflectance had insufficient contrasts to be statistically analysed. The other three comparisons showed no association between natal brightness and natal reflectance, with bright genitalia or female ornaments. It is important to note that the majority of comparisons performed could not use natal colouration due to the number of binary comparisons. Natal brightness however, can also be used as a measure of the possession of a natal pelage, as most are bright, and infants without a natal pelage are usually dull and inconspicuous. Also when sexual dichromatism is present and one sex is bright, the infants commonly resemble the duller pelage. Therefore, it is possible to consider the results for the comparisons that could only use natal pelage brightness as similar to the expected results when using natal colouration as a variable.

6.5 Results using the Binary method

Mating system, terrestriality, polygamy, female dominance and sexual dimorphism were compared with natal colouration and sexual dichromatism using the binary method. Of the ten potential comparisons, only five could be tested because five generated insufficient contrasts.

Neither mating system nor size dimorphism were associated with sexual dichromatism. This result is surprising, as the evolution of secondary sexual characteristics is considered to be associated with mate choice and intraspecific male competition for mates. These selection pressures are considered to be involved in the evolution of sexual size dimorphism (Plavcan and VanSchaik, 1997; Rodman and Mitani, 1987), and therefore, it

might be expected, that dichromatism would show similar patterns. Multi-male species are usually sexually dimorphic, as males must compete intraspecifically to gain access to females (Darwin, 1871; Selander, 1972). However, selection pressures on single male groups are likely to be at least as strong (Emlen and Lewis, 1977). The crux here is the distinction between intra- and intersexual selection. The former will effect male size, the latter colouration and ornamentation.

Neither mating system nor size dimorphism were associated with natal colouration. Multi-male species might be expected to be associated with the presence of a natal pelage if the theories concerned with male aggression were true. The paternity cloak theory proposes that promiscuity, characteristic of multi-male groups selects for natal coats (Treves, 1997). Also, if single male grouped species were correlated with natal colouration the infant defence hypothesis would have applied predicting the need for a natal coat due to male take-overs to prevent infanticide. As neither were correlated with the presence of natal colouration it seems unlikely that either hypothesis applies. Treves (1997), found limited support for both theories, but did not take into account the need to adjust for phylogenetic associations when comparing a group of species. No theories have been proposed discussing the association of sexually size dimorphic species with natal colouration. It could be postulated that there might be a possible association between the two characteristics, if aggression and dominance are directly related to an increase in male body size. If the paternity cloak hypothesis was attributed to the evolution of a natal pelage to reduce aggression and prevent infanticide, then there may have been a possible correlation. However, there is no reason why a natal pelage might reduce infanticide, as it may also increase infanticidal tendencies. Sexual size dimorphism is commonly considered to be a result of sexual selection (refer to 1.26) and provided no

support for the hypothesis that the evolution of natal colouration is associated with sexual selection.

Sexual dichromatism is significantly correlated with natal colouration and brightness. The implication of the result highlights three points. The first is that pelage brightness and pelage reflectance do not measure the same characteristic, as natal pelage reflectance did not correlate with sexual dichromatism. This matter will be discussed later. Secondly, the need to adjust for phylogenetic similarities has been illustrated with this comparison. The results of the test of independence, which did not account for the evolution of shared characteristics between closely related species, has two results that are different to those derived from CAIC or the binary method. For example, mating system correlated with natal colouration (nocturnal species removed) using the test of independence, but did not correlate using the binary method. Sexual dichromatism did not correlate with natal colouration in the standard test for independence. This study has highlighted the necessity for phylogenetic adjustment when making interspecific comparisons. The final point to consider is what the association between sexual dichromatism and natal colouration means. *Two cases seen in birds described a possible association between* sexual dichromatism and natal colouration (Darwin, 1871). The two cases describe the intimacy between sexual dichromatism and a natal pelage. One was described as the infants resembling the duller females in sexually dichromatic species. The second case is the males being duller and the infants resembling the duller males. In both cases, the infant resembles the least conspicuous sex when adult pelages are sexually dichromatic. A third case Darwin describes, is when there is no sexual dichromatism and the infants are vividly coloured. This case applies to the langurs and the black and white colobus monkey, where the infant pelages are bright (see Appendix 1.8). In the first two cases,

the infant pelage seems to actively be selected for a dull, cryptic colouration. This is often similar to the female pelage, but rarely the male pelage (except for *Eulemur fulvus rufus*). Therefore, whichever sex has been selected to be bright, infants resemble the duller sex. This reinforces the theory that one sex is sexually selected to be bright, while other individuals are cryptic. There are no instances where the adults are sexually dichromatic, and the infants have a natal pelage that is entirely different to both parents. This indicates that there are two mechanisms, where sexual selection is evolutionarily dominant over the mechanism for natal colouration.

Intraspecific Analysis

6.6 Testing the Hamilton-Zuk hypothesis in lemurs

The second part of the study examined intraspecific variation in parasite loads and pelage brightness to identify a negative correlation between pelage brightness and health as suggested by Hamilton and Zuk (1982). In an ideal situation mate choice for brighter individuals would also have been assessed unfortunately this was not possible due to costs of field work and the time scale involved. However, mate choice was not measured in the Hamilton and Zuk (1982) experimental work.

The variability in pelage reflectance between the sexes in *Lemur catta* was more than in *Eulemur fulvus rufus* (Table 5.1). There were very few correlations between oocyte load and pelage reflectance however; there were a couple of very interesting results. No significant correlations were found between parasite load and pelage reflectance in the males of either species. *E. f. rufus* females had a significant correlation between a bright pelage and the oocyte load for parasites *e* and *k*. *L. catta* females had only one significant correlation, for parasite *h*. Only oocyte *e*, identified as the oocytes of *Lemuricola,* was found in sufficient numbers and across sufficient individuals to warrant a possible relationship between the two (see Appendix 3.1). When the results from females and males from *Lemur catta* were combined, there was one significant correlation between pelage reflectance and the parasite load of oocyte *h*. A trend was also shown with the oocyte load of *Ascaris lumbricoides.* Compellingly, all the correlations reaching significance were negative, as expected.

The results between the reflectance of the chest or crown region (areas that vary in

colour in the sexually dichromatic lemur *E. f. rufus*), are more convincingly correlated with the load of the *Lemuricola* worm (Table 5.3). The wõrms were clearly visible in the faeces and were therefore much easier to count. As there were only two species of worm found (the other was *Strongyloides,* which had to be counted using a microscope), the worm of *Lemuricola* was also easy to identify. Because of these two reasons, the assessment of parasite load from the worms was more accurate. The reflectance of the crown region was significantly correlated with the worm load of *Lemuricola* in females of *E. f. rufus* and the males of *L. catta.* The crowns of *L. catta* do not appear to be different in colour, yet there is a significant correlation ($p = 0.01$) between worm number and a duller crown reflectance. One of the predictions of the Hamilton-Zuk hypothesis was that the parasite load is negatively associated with pelage reflectance, however in *L. catta* males is it positively associated (Hamilton and Zuk, 1982). The results of Figures 5.2 and 5.3 provide only partial support for the hypothesis. The correlations of *Lemuricola* oocytes and worms with the pelage reflectance of females from *E. fulvus rufus* provide stronger support for the hypothesis. The crown of females has a negative association with parasite load and the mean pelage reflectance is negatively correlated with *Lemuricola* oocytes. There is also a trend for the chest region to be negatively associated with *Lemuricola* oocytes. As in this species, it is males that are dull it would be expected, according to the Hamilton-Zuk hypothesis that there is a closer association between the parasite load and the colour of the pelage in females. This is possibly an example (and the only example) of reversed sexual dimorphism in primates.

As previously mentioned, the brightness of the pelage could be related to status, which would also correlate with parasite load. A study on *Gallus gallus*, the red junglefowl looked at the parasite loads in females and found it to correlate with status, where

females of a higher rank had fewer parasites (Zuk *et al.*, 1998). In the red junglefowl the comb size acts as a secondary sexual characteristic, where the male comb is redder and larger than in the female. No relationship was found between the comb and parasite load in females, but the association has been shown in the males that display the dimorphic features (Zuk *et al.*, 1990). Perhaps if further studies use subjects where the female has the strongest secondary sexual characteristic, a correlation would also be found between parasite susceptibility, social status and the sexual characteristic.

Although six types of endoparasite were found in both species, *Lemuricola* is the only species that can be expected to have a strong evolutionary association between the evolution of the parasite with its host. The parasite is named after the true lemurs and must therefore, be closely associated with the lifestyle and habitat of *E. f. rufus* and *L. catta*. It is therefore surprising that *Lemuricola* was not found in the wild *L. catta* samples. This does not mean however, that the parasites are not present in the wild lemurs of Madagascar. The samples were collected over a month from sites at Beza Mahafaly Special Reserve during July 1995. It was not a good time for collection of parasitic faecal samples, as this is the middle of the dry season. Parasite loads are more likely to have been high at the end of the rainy season when the parasite eggs have been consumed with food by the lemurs. Comparisons were made between captive lemurs at London Zoo and from wild lemurs in Madagascar, to ensure that the parasites found in the free ranging lemurs at DUPC were similar to those in the wild. No parasites were found in the lemurs at London zoo, despite the individuals never being preventatively treated for worms. Both of the lemurs sampled were born in captivity to captive parents, which has probably prevented the transmission of endoparasites. Only oocytes of *A. lumbricoides* were found in the faeces from the wild lemurs of Madagascar, but this was

sufficient assurance that the free-ranging lemurs at DUPC resemble the wild lemurs in terms of parasites. Most of the lemurs at DUPC were only first or second generation from the original wild lemurs; it can therefore be expected that the parasites are co-existing with the lemurs.

No difference was found between the number and type of parasites found in the dichromatic and the non-dichromatic species. The Hamilton and Zuk hypothesis (1982) predicts that the dichromatic species should be subject to a greater number of parasite species than species that do not display sexual dichromatism. This is not the case in captivity, although characteristics evolve over millenia in a taxon's characteristic habitat. Wild populations of many species would need to be analysed to be able to identify any correlation between parasite susceptibility and the evolution of sexual dichromatism. This mechanism however, may not have as much of an impact on primates as on birds, as most endoparasitic infections in primates are not deleterious to the host (Fiennes, 1967). Attempts were made to collect sufficient information on parasite loads in primates. Unfortunately, there was very little available in primates preventing further analysis.

The results concerned with the intraspecific study are summarised with the original hypotheses (Table 5.5). Hypotheses 1 and 2 must be rejected, as the results of comparisons of the coefficient of variation are greater within species (whether dichromatic or not) than between species (see above). There is some support for hypotheses three and four, which predict that parasite load should be negatively associated with pelage brightness. Very few parasite species had a significant correlation with a reflectant pelage, but there was a good correlation between *Lemuricola* load and reflectance in *E. f. rufus* females. This would be expected according to the Hamilton-Zuk

hypothesis, as *Lemuricola* has a long history of co-evolution with *E. f. rufus*, and the female is the brighter sex. *E. f. rufus* did not have a higher parasite load or a greater range of endoparasites than *L. catta,* but one of the parasites were found in the wild lemurs and not in the captive bred lemurs.

6.7 Problems encountered

One of the main problems with colouration studies is the method used to assess brightness (highlighted in the methods, section 2.2). All studies that involve quantifying a colour, be it of a plumage, scales or pelage, use a visual scale assessed by humans to describe the nature of the colour. The problem with using this method of assessment is that most animals do not share the same visual system as humans. Therefore, what we describe in terms of colour, may not refer to the colour perceived by the intended viewer of the colour. Colour has been described as a product of the brain of the animal perceiving the object, and not as an inherent property of the object (Endler, 1994). Therefore, all studies which use the visual method have a vital flaw, which is probably seriously distorting judgement on most evolutionary hypotheses involving colour (Endler, 1994). This problem is minimised in the case of primates owing to the similarity of the visual system. This study also used a physical method of measuring colour and assessing the brightness, which was provided by the spectrophotometer.

Reflectance, brightness and colour are all different phenomena (discussed in methods, section 2.2 and 2.21) section 4.4 directly compares reflectance and the visual assessment of colour to identify how the two relate to one another. Figure 4.1 shows that a visually

bright pelage colour, such as orange, does not necessarily relate to a high reflectance measurement, although white is the most reflectant colour, and black the most absorbent. The second diagram highlights how pelage colour corresponded to the visual scale (Figure 4.2). When reflectance measurements and the visual scale of pelage colours are combined, the two do show an overall trend. Higher reflectance generally corresponds with a high value of brightness (the exception being black, which is considered here to be visually bright).

Another problem encountered in using two scales was to identify which scale was the most appropriate for each requirement. Repeat reflectance measurements were made on five individuals for three species on skins at the Natural History Museum, London. This demonstrated that reflectance measurements were problematic as measures of the brightness of a species, as intraspecific variation in reflectance was in some cases larger than interspecific variation (see Appendix 1.11). The same was demonstrated when the reflectance measurements were compared inter- and intraspecifically in the two lemur species (Table 5.1). Despite one species being dichromatic (the female is of an entirely different colour to the male), the variation in reflectance between the two sexes was less than between the sexes in the species that did not display sexual dichromatism. Reflectance measurements are more suitable when used to measure intraspecific variation in pelage condition. The brightness scale is more useful as a means of describing the colouration differences between species.

There were also problems in collecting information on the ecological and behavioural lifestyle for each primate. Literature sources often conflicted in the accuracy and the nature of the information available. When the information conflicted between sources,

the most recent source was used. Often certain information was unavailable, which reduced the number of species used in some of the comparisons. Due to the large number of variables that were to be tested, a large number of comparisons were performed in the first part of the study. The number of comparisons required was reduced as much as possible to avoid the situation where, as with a very large number of comparisons, some significant results would be expected by chance. These were accounted for by performing a simple Bonferroni test to calculate the expected number of false-positive results. Multiple regressions were also performed and additional comparisons to identify if there were any confounding variables having an effect on the overall results of the comparisons. Group size did significantly appear to have a confounding effect on female pelage brightness when used in a multiple regression with sexual dimorphism, although group size did not significantly correlate with pelage brightness or with sexual size dimorphism when tested using CAIC and statistical tests.

A few limitations occurred in the second part of the study concerning data collection. The short collection time during the field study, and the nature of the free ranging environment in which faecal collections were made, limited the number of individuals that could be used. Faecal collection involved collecting the samples immediately and identifying the individual for each sample. This was often difficult, as all samples were deposited from the trees, and the only form of identification was by tag and collar. Collecting sufficient samples over a short time from individuals proved very difficult, leaving 25% of the samples unusable as there were too few per individual. The next problem was capturing the animals to make the reflectance measurements. In the free-ranging environment many individuals for which there had been sufficient faecal samples collected proved elusive, thereby further reducing the numbers in the study. There is also

a need for quantitative results on parasite infestations with regards to primate species. Unfortunately, despite continual attempts to obtain sufficient data to perform a comparative study from many sources including several veterinary colleges around the world, the information was unavailable or incomplete.

6.8 Further research

Many experiments remain to be performed concerned with testing the Hamilton-Zuk hypothesis in lemurs and other primates. A large-scale field study is required to compare parasite loads and reflectance measurements between as many individuals as possible, for several species over a length of time. The health of individuals over several years could be monitored, while faecal samples could be collected and reflectance measurements made on the same areas of the pelage. Each measurement could be taken at a specific time and associated with behavioural correlates, such as dominance, to identify further correlations between parasite load, colouration and the health of an individual. Further measurements could be made in a short-term field study on individuals in the wild. Captive animals however, especially captive-bred animals would be unsuitable for this type of study, due to the low levels of parasite infestation. Primates are the most suitable candidates for this study due to their similar visual system. It would also be better to include several species that use colour as a form of communication, such as sexually dichromatic species, or species with a natal pelage. It may be that a natal pelage allows for the same cues involving the health of the individual to be visualised.

There is also the potential for many more comparative tests using CAIC and if necessary,

the binary method of comparative analysis. Identifying associations between the variables tested in this study should be performed in other visual animals, such as birds. The mechanism of evolution of sexual dichromatism and ornamentation would be expected to be similar, although care would have to be taken when assessing the brightness of individual birds, accounting for the different visual system. Other comparative analyses could concentrate on variation in the evolution of pelage variation and brightness within smaller phylogenetic groups. The interspecific study could be combined with intraspecific measurements made on groups of individual from each species. Combining field studies with the comparative method, as in this study, will provide more insight into the mechanisms associated with the evolution of a natal pelage and sexually dichromatic features.

Chapter 7

Conclusions

7.1 Pelage colour evolution, theories in relation to the results

7.11 The evolution of sexual dichromatism and ornamentation

There are two main theories regarding the evolution of secondary sexual characteristics: the good taste hypothesis and the good sense hypothesis. The good taste hypothesis refers to the evolution of sexual dichromatism and ornamentations through female mate choice for the attractive characteristic. The good sense hypothesis describes females choosing individuals with a bright pelage and ornaments as a selective feature for health and fitness. The benefit of the good taste hypothesis is, because females choose the most attractive individuals, that the offspring will also be attractive and continue to be favoured over less attractive individuals (Fisher, 1930). This theory is now termed the "sexy son" hypothesis where females choose characters for choosing sake. If the choice for a character changes then the new characteristic will be selectively favoured. There is no method of testing this theory, but it can be accepted as the underlying mechanism for sexual selection, if the alternatives are inadequate. There are numerous variants of the handicap idea, of which the Hamilton-Zuk hypothesis is one.

In this study the Hamilton-Zuk hypothesis was tested, showing very limited support for the evolution of a bright pelage, but not for the evolution of secondary sexual characteristics in the form of sexual dichromatism. The relationship between the parasite *Lemuricola* and female reflectance in *E. f. rufus* shows a significant correlation between a bright pelage and a low incidence of both worms and oocytes. The female has a brighter pelage than the male; in this species the Hamilton-Zuk proposal relates to bright females. This pattern could have evolved through mate choice by males for the healthiest females. Females in *E. f. rufus* are the dominant sex, and pelage brightness may be used

to signal physical vigour and dominance. If the brightness of a pelage is affected by the susceptibility of an individual to parasitism, then a brighter highly ranked female will be fitter than a duller low ranked individual and should be favoured by males. From this study it is still possible that differences in patterning and colouration could be associated with species recognition, more than with sexual selection. However, highly significant results in this study strongly suggest that it is unlikely that pelage brightness and reflectant colours are associated with species recognition. Both appear to have some adaptive significance, and are therefore unlikely to be a result of 'good taste' and the heritability of fitness rather than as a result of handicap, due to low predation pressure.

Alternatives to natural selection and sexual selection for secondary sexual traits are the physiochemical hypothesis proposed by Cunningham (1900) and signal selection by Zahavi (1975). The idea that physiological effects on the body can cause the gradual evolution of a colouration could not be applied to the evolution of sexual dichromatism, as Darwin's theory is selective, whereas Cunningham's is Lamarkian. The theory had first been suggested by Darwin, with reference to the evolution of secondary sexual characteristics such as capes, manes and beards. They acted as a means of protecting vulnerable areas from attacks by other males during competition for a mate (Darwin, 1871). This study did not find any correlation between sexual dichromatism and characters that are related to intraspecific male competition, such as male grouping, group size and the presence of sexual size dimorphism. Male ornaments were not considered in this study, as most ornamented males are also sexually dichromatic. However, polygamy was associated with a bright pelage in males and females, which suggests that sexual selection is related to the evolution of a bright pelage, and not the physiological theory of Cunningham (1900). As both sexes are brighter in polygamous

species, it is likely that mate choice has caused the evolution of a bright pelage in primates. It is unlikely that a bright pelage causes a handicap (although predation may be associated). Therefore, health and parasitism may be associated with a bright pelage (Hamilton and Zuk, 1982), or both sexes could be choosing a bright pelage for aesthetic reasons i.e., a revealing handicap (Fisher, 1930). Alternatively, the bright pelage could be signalling the dominance and success of the individual, which is inherited by the offspring, who in turn, will be preferentially chosen as mates because of a bright pelage and the inheritable dominance.

A correlation between male dominance and the presence of sexual dichromatism could not be tested using the binary method, as there were insufficient contrasts. Of the few species who are female dominant, only *Eulemur fulvus rufus* is sexually dichromatic, where the female pelage is visibly brighter. If a bright pelage signals dominance, could sexual dichromatism be an extravagant display of status by the dominant sex? The signal selection hypothesis suggests the evolution of an extravagant character is caused because the higher the investment, the more reliable the signal is (Zahavi, 1975). However, a character can become so extravagant that the efficiency of the signal is reduced, as the investment in the character is more than that required to transmit the message (Zahavi, 1990). This could be the case in sexually dichromatic species where the bright pelage, which functioned as a signal of dominance and health, has evolved to an extreme form, where the two sexes display different colourations. This study however, has shown that there was no correlation between the evolution of a sexually dichromatic pelage and the brightness of either sex. It is interesting to note that in both sexes, male dominance showed a trend with the presence of bright rumps. Could this signal be related to sexual selection? If pelage brightness is not related to the presence of a sexually dichromatic

species, then the mechanism of evolution for pelage brightness must be different. The evolution of a bright pelage appears to have some relationship with dominance, and possibly health (in relation to parasite susceptibility). This feature will be inherited by mate choice selecting for a bright pelage through stabilising selection. The process of selection combines mate choice for a bright pelage which signals good health and a high ranking, the proposed mechanism is "bright pelage selection".

7.12 The evolution of natal colouration

There are many theories that have been proposed as a mechanism for the evolution of a natal pelage. The process of delayed pelage maturation in birds has been described as a signal of sub-ordinance and low status to avoid aggression and instil protective behaviour (Andersson, 1994). A suggestion named "female mimicry" highlights the use of a female pelage in infants to signal the low status of the infant in the troop (Rohwer *et al.*, 1980). This theory can be applied to many cases in primates where sexual dichromatism is present. The infant pelage closely resembles the least dominant sex, which is often the female. The males are brighter, possibly to signal their status, and the females are a dull and less conspicuous colour. Only in *E. f. rufus* does the female appear brighter than the male; here, the females are dominant and the infants resemble the males. The significant association between male and female pelage brightness and the evolution of a natal pelage does not support the female mimicry hypothesis. It is apparent that there are two forms of natal colouration. One is associated with the evolution of sexual dichromatism, where the infant resembles the least dominant sex in pelage colour, and one where the infant is often bright when sexual dichromatism is absent. The dull colour of an infant in

a sexually dichromatic species may reduce aggression from the dominant sex by signalling low rank. The significant correlation of sexual dichromatism and natal colouration is perhaps due to this evolutionary relationship.

The second form of communication using a natal pelage is when the sexes are similar, and the infant is brightly coloured, or visibly different. This case applies to the langurs *Colobus polykomos* (the black and white colobus), *Nasalis larvatus* (the proboscis monkey), *Cercopithecus neglectus* (De Brazza's monkey), *Erythrocebus patas* (the patas monkey), and *Ateles geoffroyi* (the black handed spider monkey). Some macaques and baboons display a natal colouration, where the pelage is darker than the adult pelage. *Callimico goeldi* (Goeldi's monkey), and *Eulemur macaco* (the black lemur) have a natal pelage that is grey, duller than the black adult pelage. Some infants do not have a pelage colouration, but use ornaments to communicate the ontogenetic signal; for example, rump tufts in chimps and gorillas, and hair partings in some macaques. Results from this study show that where aggression is common, there are no correlations with pelage colouration. It is possible that, in some species, ontogenetic signalling reduces aggression as one (but not the sole) purpose for the evolution of a natal pelage. Allomothering also appears to be one of the factors associated with a natal pelage, but it cannot be the sole purpose of the pelage, as the ring-tailed lemur and some capuchins practice allocare without the presence of a natal coat, and there is no general relationship with natal coats (Ross and Regan, in press). It is therefore suggested that a natal pelage can serve many functions, where each is dependent on the needs of the species. The evolution of the natal coat and the use of ornaments may have selectively evolved from the development of the lower ranked sex pelage when sexual dichromatism is present, due to the favourable selective responses. More likely, sexual dichromatism evolved through one

sex becoming bright, while infants and the other sex remained dull. Alternatively, bright natal pelages may have changed to resemble the sub-ordinate sex in dichromatic species to reduce adult aggression towards the infants, although two evolutionary events seem unlikely. Many primates do not have a natal pelage, yet the infants are cared for and nurtured, many reaching adulthood to propagate the species. Therefore, additional features to those that are common to newborns such as size, smell and the cry are unnecessary to instil maternal behaviour in many primates.

7.2 Implications

The aim of the study was to identify correlates of inter- and intraspecific pelage variation in primates, manifested in the forms of brightness, sexual dichromatism, ornamentation and natal colouration. These pelage colourations are used to signal ontogenetic and sexual differences between individuals. Many behavioural and ecological characteristics showed no correlation with the evolution of sexually dichromatic features, or with the possession of a natal pelage. The comparative results suggest the two forms of pelage colouration may be related. No hypotheses concerning the evolution of intraspecific pelage colourations in mammals have previously been tested using the comparative method and adjusting for the evolution of characters by descent. Pelage brightness and dichromatism are not strongly related. Mechanisms have been suggested for the evolution of a bright pelage and for the evolution of sexual dichromatism. At least two forms of natal colouration have been identified; one of which is associated with the presence of sexual dichromatism. The evolution of a bright natal pelage in species that do not display sexual dichromatism may be associated with several behavioural

characteristics that are dependent on the ecology of the species. The usefulness of a spectrophotometer for the analysis of intraspecific variation in pelage condition has been highlighted.

The functional hypotheses which are listed in Table 1.1, showed predictions which could apply to the evolution of primate pelage colouration. In the literature most of the functional hypotheses had not been tested and of those which had, none had accounted for the impact of phylogenetic differences when conducting comparative analyses. Therefore, differences between proposed or previously expected hypotheses, and the results in this study are to be expected. The differences in approach to phylogenetic analysis were demonstrated in this study by performing three different comparative tests, one of which was non-phylogenetic. Results illustrated how adjusting for the evolution of a character between closely and distantly related species adjusted the outcome of the correlation, e.g.; when comparing strepshirines and platyrrhines the evolution of colour appears to be different. The implications of this study validates the use of phylogenetic adjustment by independent contrasts and highlights the need for further research to be conducted into the evolution of primate coat colouration.

Appendices

CONTENTS

Species	Count	Crown	Cheek	Chest	Back	Outer Leg	Rump	Total	$\bar{\chi}$	σ
Saimiri	1	4	45	38	7	16	13			
oerstedii	2	5	40	36	8	15	10			
	Mean	4.5	42.5	37	7.5	15.5	11.5	118.5		
	1	4	14	18	9	14	8			
	2	3	14	24	6	14	7			
	Mean	3.5	14	21	7.5	14	7.5	67.5		
	1	4	26	28	11	21	9			
	2	3	25	30	8	18	8			
	Mean	3.5	25.5	29	9.5	19.5	8.5	95.5		
	1	5	30	30	9	15	10			
	2	5	31	35	6	15	10			
	Mean	5	30.5	32.5	7.5	15	10	100.5		
	1	4	22	14	9	14	19			
	2	3	24	16	10	13	19			
	Mean	3.5	23	15	9.5	13.5	19	83.5	93.1	19.06
Colobus	1	3	43	4	4	18	8			
polykomos	2	2	41	3	4	18	6			
	Mean	2.5	42	3.5	4	18	7	77		
	1	3	56	4	5	19	5			
	2	3	49	4	4	19	4			
	Mean	3	52.5	4	4.5	19	4.5	87.5		
	1	4	40	3	3	23	4			
	2	4	42	4	3	23	4			
	Mean	4	41	3.5	3	23	4	72.5		
	1	4	50	4	4	19	4			
	2	3	48	4	5	20	4			
	Mean	3.5	49	4	4.5	19.5	4	84.5		
	1	4	37	4	4	25	5			
	2	3	43	4	4	21	5			
	Mean	3.5	40	4	4	23	5	79.5	80.2	5.95
Cheirogaleus	1	18		48	16	20	17			
medius	2	20		47	18	21	19			
	Mean	19		47.5	17	20.5	18	122		
	1	18		41	11	15	14			
	2	22		36	13	12	14			
	Mean	20		38.5	12	13.5	14	98		
	1	14		42	19	12	16			
	2	10		40	14	15	16			
	Mean	12		41	16.5	13.5	16	99		
	1	14		40	16	17	16			
	2	15		40	15	17	16			
	Mean	14.5		40	15.5	17	16	103	105.5	11.2

σ of intraspecific variation is 19.06, 5.95, 11.20

σ of interspecific variation is 12.65

Appendix 1.11: Replicates of reflectance measurements

Species	S/A	Count	Crown	Cheek	Chest	Back	Out. Leg	Rump
Allenopithecus nigroviridis	M/A	1	6	6	27	8	10	9
		2	6	7	31	6	8	8
		Mean	6	6.5	29	7	9	8.5
Allenopithecus nigroviridis	F/A	1	5	10	23	7	5	8
		2	5	9	23	6	7	9
		Mean	5	9.5	23	6.5	6	8.5
Alouatta caraya	M/A	1	4	3	7	3	4	4
		2	4	3	8	3	3	3
		Mean	4	3	7.5	3	3.5	3.5
Alouatta caraya	F/A	1	18	14	15	24	9	20
		2	15	16	16	27	10	20
		Mean	16.5	15	15.5	25.5	9.5	20
Alouatta fusca	M/A	1	5	6	6	8	6	6
		2	6	6	5	12	6	6
		Mean	5.5	6	5.5	10	6	6
Alouatta fusca	F/A	1	4	6	5	4	3	4
		2	4	6	6	3	2	4
		Mean	4	6	5.5	3.5	2.5	4
Aotus trivirgatus	M/A	1	3		31	8	10	10
		2	4		32	8	9	7
		Mean	3.5		31.5	8	9.5	8.5
Aotus trivirgatus	F/A	1	6		33	9	13	13
		2	6		29	8	11	11
		Mean	6		31	8.5	12	12
Ateles geoffroyi	M/A	1	4	8	11	6	4	5
		2	4	9	10	7	3	5
		Mean	4	8.5	10.5	6.5	3.5	5
Ateles geoffroyi	F/A	1	3	7	8	4	3	5
		2	4	5	6	4	3	6
		Mean	3.5	6	7	4	3	5.5
Cacajao calvus	M/A	1	19	15	10	30	17	26
		2	17	14	11	25	19	29
		Mean	18	14.5	10.5	27.5	18	27
Cacajao calvus	F/A	1	10	15	14	36	25	29
		2	13	16	13	32	26	28
		Mean	11.5	15.5	13.5	34	25.5	28.5
Callicebus torquatus	M/A	1	4	5	7	5	5	5
		2	5	6	9	5	5	5
		Mean	4.5	5.5	8	5	5	5
Callicebus torquatus	F/A	1	3	5	10	5	7	5
		2	4	4	13	5	9	4
		Mean	3.5	4.5	11.5	5	8	4.5
Callimico goeldi	M/A	1	4	4	3	4	5	6
		2	3	4	3	4	6	6
		Mean	3.5	4	3	4	5.5	6
Callimico goeldi	F/A	1	3	3	4	3	5	9
		2	3	4	4	3	5	8
		Mean	3	3.5	4	3	5	8.5

Appendix 1.12: Reflectance measurements made on skins from the Natural History Museum, London

Species	S/A	Count	Crown	Cheek	Chest	Back	Out. Leg	Rump
Cebus apella	M/A	1	3	8	9	4	8	4
		2	3	9	7	4	6	6
		Mean	3	8.5	8	4	7	5
Cebus apella	F/A	1	3	25	33	4	6	5
		2	3	20	27	4	5	5
		Mean	3	22.5	30	4	5.5	5
Cebus apella	F/N	1	5	20	22	4	24	13
		2	6	21	21	4	19	9
		Mean	5.5	20.5	21.5	4	21.5	11
Cebus capucinus	M/A	1	13	12	22	2	3	2
		2	10	13	20	1	4	2
		Mean	11.5	12.5	21	1.5	3.5	2
Cebus capucinus	F/A	1	18	22	12	3	4	3
		2	19	20	13	3	3	3
		Mean	18.5	21	12.5	3	3.5	3
Cebus capucinus	M/N	1	23	11	12	2	5	3
		2	20	15	13	2	6	2
		Mean	21.5	13	12.5	2	5.5	2.5
Cercopithecus neglectus	M/A	1	5	10	6	10	26	14
		2	4	9	5	13	26	13
		Mean	4.5	9.5	5.5	11.5	26	13.5
Cercopithecus neglectus	F/A	1	13	10	8	12	11	20
		2	12	10	9	12	9	18
		Mean	12.5	10	8.5	12	10	19
Cercopithecus neglectus	M/J	1	7		31	8	20	13
		2	9		36	8	18	13
		Mean	8		33.5	8	19	13
Cercopithecus neglectus	F/J	1	7		31	10	19	10
		2	8		35	8	16	10
		Mean	7.5		33	9	17.5	10
Cheirogaleus medius	M/A							
		4 replicates						
		Mean	17		31	16	17	17
Cheirogaleus medius	F/A	1	12		40	12	20	18
		2	10		43	12	18	17
		Mean	11		41.5	12	19	17.5
Cheirogaleus medius	M/N	1	12		30	30	20	17
		2	12		35	24	21	16
		Mean	12		32.5	27	20.5	16.5
Colobus polykomos	M/J	1	3	38	5	4	15	4
		2	4	36	6	3	14	4
		Mean	3.5	37	5.5	3.5	14.5	4
Colobus polykomos	F/A	1	5	38	4	5	17	5
		2	4	33	5	5	16	5
		Mean	4.5	35.5	4.5	5	16.5	5
Colobus polykomos	F/N	1	35		23	20	17	13
		2	37		20	19	17	14
		Mean	36		21.5	20.5	17	13.5
Colobus polykomos	M/A	5 replicates						
		Mean	3.5	48.5	4	4	20.5	6

Appendix 1.12 (cont): Reflectance measurements made on skins from the Natural History Museum, London

Species	S/A	Count	Crown	Cheek	Chest	Back	Out. Leg	Rump
Daubentonia	M/A	1	6	5	18	19	4	3
madagascarensis		2	4	6	15	19	3	2
		Mean	5	5.5	16.5	19	3.5	2.5
Eulemur fulvus	M/A	1	2	7	25	7	12	8
		2	1	5	26	7	13	9
		Mean	1.5	6	25.5	7	12.5	8.5
Eulemur fulvus	F/A	1	2	3	24	7	12	8
		2	2	3	26	6	11	8
		Mean	2	3	25	6.5	11.5	8
Eulemur macaco	M/A	1	2	3	6	2	5	2
		2	1	3	6	3	4	2
		Mean	1.5	3	6	2.5	4.5	2
Eulemur macaco	F/A	1	10	26	24	12	27	15
		2	6	25	25	11	21	18
		Mean	8	25.5	24.5	11.5	24	17.5
Eulemur mongoz	M/A	1	5	27	23	5	17	13
		2	4	30	19	5	17	11
		Mean	4.5	28.5	21	5	17	12
Eulemur mongoz	F/A	1	9	25	28	9	17	9
		2	10	30	30	8	15	10
		Mean	9.5	27.5	29	8.5	16	9.5
Eulemur mongoz	M/J	1	3		20	5	9	8
		2	5		24	5	10	9
		Mean	4		22	5	9.5	8.5
Hylobates agilis	M/A	1	3	7	3	3	3	4
		2	2	8	3	4	4	3
		Mean	2.5	7.5	3	3.5	3.5	3.5
Hylobates agilis	F/A	1	4	15	4	5	3	4
		2	4	11	3	7	3	5
		Mean	4	13	3.5	6	3	4.5
Hylobates agilis	M/J	1	3	18	4	3	6	5
		2	3	20	4	2	5	5
		Mean	3	19	4	2.5	5.5	5
Hylobates concolor	M/A	1	2	5	3	2	4	4
		2	2	4	3	2	3	4
		Mean	2	4.5	3	2	3.5	4
Hylobates concolor	F/A	1	16	16	16	15	17	16
		2	14	18	13	17	20	12
		Mean	15	17	14.5	16	18.5	14
Hylobates concolor	M/J	1	12	15	10	14	23	6
		2	12	13	12	14	24	5
		Mean	12	14	11	14	23.5	5.5
Hylobates concolor	F/J	1	5	35	16	3	8	4
		2	3	36	20	3	5	4
		Mean	4	35.5	18	3	6.5	4

Appendix 1.12 (cont): Reflectance measurements made on skins from the Natural History Museum, London

Species	S/A	Count	Crown	Cheek	Chest	Back	Out. Leg	Rump
Hylobates hoolock	M/A	1	5	5	5	5	4	5
		2	4	4	5	5	5	4
		Mean	4.5	4.5	5	5	4.5	4.5
Hylobates hoolock	F/A	1	20	7	4	10	17	12
		2	20	8	5	11	16	10
		Mean	20	7.5	4.5	10.5	16.5	11
Hylobates lar	M/A	1	3	20	5	5	5	6
		2	2	18	5	6	5	6
		Mean	2.5	19	5	5.5	5	6
Hylobates lar	F/A	1	17	25	21	22	17	14
		2	16	29	22	19	17	13
		Mean	16.5	27	21.5	20.5	17	13.5
Hylobates lar	M/J	1	32	17	9	30	27	30
		2	34	16	8	31	27	33
		Mean	33	16.5	8.5	30.5	27	31.5
Hylobates lar	F/N	1	7	12	6	9	12	19
		2	9	11	6	9	11	17
		Mean	8	11.5	6	9	11.5	18
Hylobates pileatus	M/A	1	3	17	3	4	4	35
		2	2	14	4	3	4	36
		Mean	2.5	15.5	3.5	3.5	4	35.5
Hylobates pileatus	F/A	1	4	6	2	20	15	17
		2	4	6	3	17	14	19
		Mean	4	6	2.5	18.5	14.5	18
Hylobates pileatus	M/J	1	11	30	30	20	28	29
		2	10	25	34	21	24	29
		Mean	10.5	27.5	32	20.5	26	29
Hylobates syndactylus	M/A	1	1	3	4	4	3	4
		2	2	2	4	4	4	4
		Mean	1.5	2.5	4	4	3.5	4
Hylobates syndactylus	F/A	1	3	9	3	3	3	3
		2	2	8	3	4	4	3
		Mean	2.5	8.5	3	3.5	3.5	3
Indri brevicaudatus	M/A	1	3	7	8	3	4	37
		2	1	5	10	2	4	39
		Mean	2	6	9	2.5	4	38
Indri brevicaudatus	F/A	1	1	20	7	2	4	45
		2	2	19	7	3	6	48
		Mean	1.5	19.5	7	2.5	5	46.5
Indri brevicaudatus	M/N	1	3	12	3	3	3	24
		2	3	10	5	2	3	25
		Mean	3	11	4	2.5	3	24.5
Indri brevicaudatus	F/N	1	3	7	5	3	3	17
		2	4	8	5	3	3	24
		Mean	3.5	7.5	5	3	3	20.5
Lemur catta	M/A	1	1	14	10	1	1	44
		2	2	16	14	2	1	39
		Mean	1.5	15	12	1.5	1	42.5
Lemur catta	F/A	1	8	37	29	15	15	14
		2	6	38	24	16	13	17
		Mean	7	37.5	26.5	8.5	14	15.5
Lemur catta	M/J	1	10		36	15	25	20
		2	11		37	17	25	19
		Mean	10.5		36.5	16	25	19.5

Appendix 1.12 (cont): Reflectance measurements made on skins from the Natural History Museum, London

Species	S/A	Count	Crown	Cheek	Chest	Back	Out. Leg	Rump
Leontopithecus rosalia	M/A	1	24	44	19	33	15	27
		2	30	43	19	34	14	24
		Mean	28	43.5	19	33.5	14.5	25.5
Leontopithecus rosalia	F/A	1	14	40	17	26	11	24
		2	14	41	14	28	10	26
		Mean	14	40.5	15.5	27	10.5	25
Macaca fascicularis	M/A	1	11	6	17	7	14	7
		2	10	7	19	8	13	5
		Mean	10.5	6.5	18	7.5	13.5	6
Macaca fascicularis	F/A	1	10	17	8	9	14	8
		2	8	16	7	9	14	8
		Mean	9	16.5	7.5	9	14	8
Macaca fascicularis	M/J	1	7	21	24	8	21	15
		2	8	20	26	8	26	17
		Mean	7.5	20.5	25	8	23.5	16
Macaca mulatta	M/A	1	10	13	11	10	18	12
		2	9	11	9	9	16	12
		Mean	9.5	12	10	9.5	17	12
Macaca mulatta	F/A	1	9	10	7	8	11	12
		2	9	11	7	9	13	10
		Mean	9	10.5	7	8.5	12	11
Mandrillus sphinx	M/A	1	4	20	3	5	5	18
		2	5	25	5	4	4	19
		Mean	4.5	22.5	4	4.5	4.5	18.5
Mandrillus sphinx	F/A	1	7	14	23	5	11	6
		2	8	14	25	5	13	6
		Mean	7.5	14	24	5	12	6
Nasalis larvatus	M/A	1	7	20	31	9	15	19
		2	8	18	31	10	17	16
		Mean	7.5	19	31	9.5	16	17.5
Nasalis larvatus	F/N	1	13	16	30	15	17	19
		2	12	17	29	14	18	12
		Mean	12.5	16.5	29.5	14.5	17.5	15.5
Papio papio	M/A	1	7	15	10	5	9	12
		2	5	14	11	5	8	15
		Mean	6	14.5	10.5	5	8.5	13.5
Papio papio	F/J	1	7	11	12	9	17	22
		2	9	10	10	6	16	20
		Mean	8	10.5	11	7.5	16.5	21
Papio ursinus	M/A	1	4	7	13	4	7	9
		2	5	8	12	5	11	10
		Mean	4.5	7.5	12.5	4.5	9	10.5
Papio ursinus	F/A	1	8	15	9	7	7	13
		2	9	14	9	6	5	11
		Mean	8.5	14.5	9	6.5	6	12
Pithecia monachus	M/A	1	6	8	11	5	4	6
		2	6	7	9	6	4	6
		Mean	6	7.5	10	5.5	4	6
Pithecia monachus	F/A	1	5	13	7	6	5	5
		2	9	9	9	6	5	6
		Mean	7	11	8	6	5	5.5

Appendix 1.12 (cont): Reflectance measurements made on skins from the Natural History Museum, London

Species	S/A	Count	Crown	Cheek	Chest	Back	Out. Leg	Rump
Pithecia monachus	M/N	1	10	13	20	5	5	6
		2	11	11	23	5	5	5
		Mean	10.5	12	21.5	5	5	5.5
Pithecia pithecia	M/A	1	29	20	6	5	4	5
		2	33	23	7	4	4	5
		Mean	31	21.5	6.5	4.5	4	65
Pithecia pithecia	F/A	1	5	8	10	4	6	5
		2	6	9	14	3	6	6
		Mean	5.5	8.5	12	3.5	6	5.5
Pongo pygmaeus	M/A	1	4	7	4	5	5	6
		2	5	8	4	3	5	4
		Mean	4.5	7.5	4	4	5	5
Pongo pygmaeus	F/A	1	6	7	4	6	5	6
		2	5	8	5	4	4	4
		Mean	5.5	7.5	4.5	5	4.5	5
Presbytis cristata	M/A	1	7	7	8	5	7	5
		2	6	5	6	6	6	6
		Mean	6.5	6	7	5.5	6.5	5.5
Presbytis cristata	F/A	1	6	8	15	5	7	5
		2	6	7	13	6	8	4
		Mean	6	7.5	14	5.5	7.5	4.5
Presbytis cristata	F/N	1	34		23	24	36	26
		2	33		24	21	45	24
		Mean	33.5		23.5	22.5	40.5	25
Presbytis phayrei	M/A	1	7	7	15	7	13	7
		2	8	6	16	6	9	6
		Mean	7.5	6.5	15.5	6.5	11	6.5
Presbytis phayrei	F/A	1	7	10	16	6	8	6
		2	8	10	14	6	8	6
		Mean	7.5	10	15	6	8	6
Presbytis phayrei	M/N	1	18		23	14	13	15
		2	17		22	12	12	15
		Mean	17.5		22.5	13	12.5	15
Presbytis pileata	M/A	1	8	9	12	8	15	11
		2	8	12	14	6	21	14
		Mean	8.5	10.5	13	7	18	12.5
Presbytis pileata	F/A	1	8	13	16	7	15	21
		2	8	14	18	6	15	11
		Mean	8	13.5	17	6.5	15	16
Presbytis pileata	M/N	1	20		30	24	28	16
		2	16		30	22	25	12
		Mean	18		30	21	26.5	14

Appendix 1.12 (cont): Reflectance measurements made on skins from the Natural History Museum, London

Species	S/A	Count	Crown	Cheek	Chest	Back	Out. Leg	Rump
Presbytis obscura	M/A	1	9	10	20	10	7	7
		2	6	9	28	13	8	7
		Mean	7.5	9.5	24	11.5	7.5	7
Presbytis obscura	F/A	1	15	6	15	24	10	11
		2	17	5	19	21	9	10
		Mean	16	5.5	17	22.5	9.5	10.5
Presbytis obscura	M/N	1	17	16	17	14	26	17
		2	16	18	17	6	29	17
		Mean	16.5	17	17	10	27.5	17
Presbytis obscura	F/J	1	11	14	20	5	25	7
		2	15	18	24	6	15	7
		Mean	13	16	22	5.5	20	7
Pygathrix nemaeus	M/A	1	9	30	11	11	4	51
		2	7	26	8	13	4	39
		Mean	8	28	9.5	12	4	50
Pygathrix nemaeus	F/A	1	4	14	7	9	5	24
		2	5	12	8	9	4	29
		Mean	4.5	13	7.5	9	4.5	26.5
Pygathrix nemaeus	F/J	1	4	24	18	10	5	24
		2	5	23	19	11	4	29
		Mean	4.5	23.5	18.5	10.5	4.5	26.5
Pygathrix roxellanae	M/A	1	6	10	24	15	10	33
		2	6	12	24	12	12	30
		Mean	6	11	24	13.5	11	31.5
Pygathrix roxellanae	F/A	1	20	24	24	11	21	10
		2	19	24	23	12	24	7
		Mean	19.5	24	23.5	11.5	22.5	8.5
Pygathrix roxellanae	F/J	1	8		26	20	15	20
		2	10		28	16	19	26
		Mean	9		27	18	17	23
Saguinus bicolor	M/A	1	28	2	44	59	12	11
		2	27	3	40	63	13	15
		Mean	27.5	2.5	42	61	12.5	13
Saguinus bicolor	F/A	1	36	3	47	44	12	10
		2	40	4	43	40	13	11
		Mean	38	3.5	45	42	12.5	10.5
Saguinus mystax	M/A	1	3	18	4	2	4	4
		2	5	15	3	3	4	5
		Mean	4	16.5	3.5	2.5	4	4.5
Saguinus mystax	F/A	1	3	20	16	4	5	7
		2	6	21	16	4	5	6
		Mean	4.5	20.5	16	4	5	6.5
Saimiri oerstedii	M/A							
		5 replicates						
		Mean	4	27	26	8.5	16	11
Saimiri oerstedii	F/A	1	5	32	33	10	14	10
		2	5	30	35	9	15	10
		Mean	5	31	34	9.5	14.5	10

Appendix 1.12 (cont): Reflectance measurements made on skins from the Natural History Museum, London

Species	S/A	Count	Crown	Cheek	Chest	Back	Out. Leg	Rump
Tarsius bancanus	M/A	1	9		16	10	13	14
		2	11		11	7	15	13
		Mean	10		13.5	8.5	14	13.5
Tarsius bancanus	F/A	1	11		11	10	14	19
		2	9		13	10	13	18
		Mean	10		12	10	13.5	18.5

Appendix 1.12 (cont): Reflectance measurements made on skins from the Natural History Museum, London

Ho: There is no difference between reflectance measurements from live and dead individuals of the same species

Mann-Whitney U test (Siegal and Castellan, 1988)

n-live *m*-dead *Lemur catta*

Ho: P[X > Y] = ½.

n = 10, 5 male and 5 female individuals
m = 2, 1 male and 1 female individual

Body part	W_x	Significance
Crown	8.5	x
Chest	7.5	x
Cheek	9	x
Back	19	x
Outer Leg	5	x
Rump	4	x

W_x = Rank sum of m
x = not significant at $p > 0.05$ (W_x between 4 and 22)

The reflectance measurements of X and Y are not significantly different, therefore *Ho* is accepted

Appendix 1.13: Comparison of live versus dead pelage reflectance measurements for *Lemur catta*

Species	°omale weight	Av. group size	Activity	Sex. Dichrom.	Natal col.	Male grouping	mon/pol	arb/terr	Male dom.	Size dimorph.	Bright genitalia	Female ornaments
Allenopithecus nigroviridis	85.42	2	1	0	0	0	0	0	0	1	1	0
Alouatta belzebul	77.4	-9	1	0	0	-9	1	0	0	1	0	0
Alouatta caraya	85	8	1	1	1	1	1	0	0	1	0	0
Alouatta fusca	-9	-9	1	1	1	-9	1	0	0	1	0	0
Alouatta palliata	77.03	9	1	0	0	1	1	0	0	1	0	0
Alouatta seniculus	79.01	8.1	1	0	0	1	1	-9	0	1	0	0
Alouatta villosa	-9	5	1	0	0	0	-9	-9	-9	1	0	0
Ateles belzebuth	93.55	19	1	0	0	1	1	0	0	0	0	0
Ateles fusciceps	102.25	-9	1	0	0	1	1	0	0	0	0	0
Ateles geoffroyi	93.55	17	1	0	1	1	1	0	0	0	0	0
Ateles paniscus	87.88	18	1	0	0	1	1	0	0	1	0	0
Brachyteles arachnoides	100	22	1	0	0	1	1	0	0	0	0	0
Cacajao calvus	86.96	20	1	0	0	1	-9	0	0	1	0	0
Cacajao melanocephalus	100	20	1	0	0	1	-9	0	0	0	0	0
Callicebus moloch	95.45	3.3	1	0	0	-9	0	0	0	0	0	0
Callicebus personatus	100	4	1	0	0	-9	0	0	0	0	0	0
Callicebus torquatus	100	3	1	0	0	-9	0	0	0	0	0	0
Callimico goeldii	81.54	7.2	1	0	1	0	-9	0	0	1	0	0
Callithrix argentata	96.15	-9	1	0	0	1	-9	0	0	0	1	0
Callithrix humeralifer	100	9	1	0	0	1	-9	0	0	0	1	0
Callithrix jacchus	93.55	9	1	0	0	1	-9	0	0	0	1	0
Cebuella pygmaea	87.5	6	1	0	0	0	-9	0	0	0	1	0
Cebus albifrons	100	35	1	0	0	1	-9	0	0	0	0	1
Cebus apella	73.43	13	1	0	0	1	1	0	0	1	0	0
Cebus capucinus	71.05	15	1	0	0	0	1	1	0	1	0	1
Cebus olivaceus	-9	18	1	0	0	0	1	1	0	1	0	0
Cercocebus albigena	71.11	15.7	1	0	0	1	1	1	0	1	0	0
Cercocebus aterrimus	-9	-9	1	0	0	1	1	1	0	1	0	0
Cercocebus atys	53.92	35	1	0	0	1	1	1	0	1	0	0
Cercocebus galeritus	53.92	26	1	0	0	1	1	1	0	1	0	0
Cercocebus torquatus	68.75	-9	1	0	0	1	1	1	0	1	0	0
Cercopithecus aethiops	74.95	24	1	0	0	1	1	1	0	1	1	0
Cercopithecus ascanius	69.05	28.1	1	0	0	0	1	1	0	1	0	0
Cercopithecus campbelli	100	-9	1	0	0	0	1	1	0	0	0	0

Appendix 1.2: Ecological and behavioural variables for diurnal primates

Species	%male weight	Av. group size	Activity	Sex. Dichrom.	Natal col.	Male grouping	mon/pol	arb/terr	Male dom.	Size dimorph.	Bright genitalia	Female ornaments
Cercopithecus cephus	70.73	-9	1	0	0	0	1	1	1	1	0	0
Cercopithecus diana	-9	-9	1	0	0	0	1	1	1	1	1	0
Cercopithecus erythrogaster	-9	-9	1	0	0	0	1	1	1	1	0	0
Cercopithecus erythrotis	-9	-9	1	0	0	0	1	1	1	1	0	0
Cercopithecus hamlyni	-9	-9	1	0	0	0	0	0	1	1	0	0
Cercopithecus lhoesti	55.29	-9	1	0	0	0	1	1	1	1	0	0
Cercopithecus mitis	57.89	18.7	1	0	0	0	1	1	1	1	0	0
Cercopithecus mona	56.82	-9	1	0	0	0	1	1	1	1	0	0
Cercopithecus neglectus	56.57	-9	1	0	1	0	0	0	1	1	0	0
Cercopithecus nictitans	63.64	-9	1	0	0	0	1	1	1	1	1	0
Cercopithecus petaurista	-9	-9	1	0	0	0	1	1	1	1	0	0
Cercopithecus pogonias	66.67	-9	1	0	0	0	-9	-9	1	1	0	0
Chiropotes albinasus	80.45	25	1	0	0	1	-9	0	1	1	1	0
Chiropotes satanas	-9	-9	1	0	0	1	-9	0	1	0	1	0
Colobus angolensis	84.11	-9	1	0	1	0	1	0	1	0	0	0
Colobus badius	55.24	-9	1	0	0	1	1	0	1	1	0	0
Colobus guereza	78.39	12	1	0	1	0	1	0	1	1	0	0
Colobus polykomos	80.77	-9	1	0	1	0	1	0	1	1	0	0
Colobus satanus	79.17	15	1	0	1	1	1	0	1	1	0	0
Colobus vellerosus	-9	-9	1	0	0	1	-9	0	1	1	0	0
Erythrocebus patas	56	35.5	1	0	1	0	-9	0	1	1	1	0
Gorilla gorilla	58.12	10	1	1	0	0	1	1	1	1	0	0
Hapalemur griseus	100	4	1	0	0	-9	0	0	1	0	0	0
Hapalemur simus	100	4	1	0	0	-9	0	0	1	0	0	0
Hylobates agilis	95	4.4	1	0	0	-9	0	0	1	0	0	1
Hylobates concolor	103.57	3.5	1	1	1	-9	0	0	1	0	0	0
Hylobates hoolock	94.2	3.2	1	1	1	-9	0	0	1	0	0	0
Hylobates klossi	103.51	3.8	1	0	0	-9	0	0	1	0	0	0
Hylobates lar	92.98	4	1	0	0	-9	0	0	1	0	0	0
Hylobates moloch	95	-9	1	0	0	-9	0	0	1	0	1	0
Hylobates muelleri	100	3.4	1	0	0	-9	0	0	1	0	0	0
Hylobates pileatus	-9	3.7	1	1	1	-9	0	0	1	0	1	0
Hylobates syndactylus	97.25	4	1	0	0	-9	0	0	0	0	1	0
Indri indri	100	3	1	0	0	-9	0	0	1	0	0	0
Lagothrix flavicauda	60	9.1	1	0	0	1	1	0	1	1	1	0

Species	°omale weight	Av. group size	Activity	Sex. Dichrom.	Natal col.	Male grouping	mon/pol	arb terr	Male dom.	Size dimorph.	Bright genitalia	Female ornaments
Lemur catta	86.21	17	1	0	0	1	1	1	0	0	0	0
Leontopithecus rosalia	98.21	5	1	0	0	1	-9	0	1	0	0	0
Macaca arctoides	86.96	-9	1	0	1	1	1	1	1	1	0	0
Macaca assamensis	64.02	12	1	0	0	1	1	0	1	1	0	0
Macaca cyclopis	-9	-9	1	0	0	1	1	0	1	1	0	0
Macaca fascicularis	69.49	27	1	0	1	1	1	0	1	1	0	0
Macaca fuscata	77.78	36.6	1	0	1	1	1	0	1	1	0	0
Macaca mulatta	48.38	35.5	1	0	0	1	1	0	0	1	0	0
Macaca nemestrina	75	18.3	1	0	0	1	1	0	1	1	0	0
Macaca nigra	60	-9	1	0	1	1	1	0	1	1	0	0
Macaca radiata	56.06	34.5	1	0	1	1	1	0	1	1	0	0
Macaca silenus	73.53	-9	1	0	0	1	1	0	1	1	0	0
Macaca sinica	52.31	24.8	1	0	0	1	1	0	1	1	0	0
Macaca sylvanus	89.28	-9	1	0	0	1	1	0	1	1	0	0
Mandrillus leucophaeus	58.82	17.5	1	0	0	0	1	1	1	1	1	0
Mandrillus sphinx	55.58	13.9	1	1	1	0	1	1	1	1	1	0
Miopithecus talapoin	60.16	76.9	1	0	0	1	1	0	0	1	0	0
Nasalis larvatus	48.77	20	1	0	1	1	1	-9	1	1	0	0
Pan paniscus	83.03	-9	1	0	1	1	1	1	1	1	0	0
Pan troglodytes	74.76	28	1	0	0	1	1	1	1	1	1	0
Papio anubis	57.14	45	1	0	0	1	1	1	1	1	0	0
Papio cynocephalus	75	40.5	1	0	1	1	1	1	1	1	0	0
Papio hamadryas	43.72	7.3	1	1	1	1	1	1	1	1	0	0
Papio papio	50	-9	1	0	1	1	1	1	1	1	0	0
Papio ursinus	82.35	47.2	1	0	1	1	1	1	1	1	0	0
Petterus coronatus	100	-9	1	1	0	0	-9	0	1	0	0	0
Petterus fulvus	76	9	1	1	0	1	0	0	1	1	0	0
Petterus macaco	100	10	1	1	1	1	0	0	1	0	0	0
Petterus mongoz	100	2	1	1	0	-9	0	0	1	0	0	1
Petterus rubriventer	100	2	1	1	0	-9	0	0	1	0	0	0
Pithecia monachus	78.57	3	1	0	0	-9	0	0	1	1	0	1
Pithecia pithecia	87.5	3	1	1	0	-9	0	0	1	1	0	0
Pongo pygmaeus	53.62	-9	1	0	0	-9	1	0	1	1	0	0

Appendix 1.2 (cont): Ecological and behavioural variables for diurnal primates

Species	%male weight	Av. group size	Activity	Sex. Dichrom.	Natal col.	Male grouping	mon/pol	arb/terr	Male dom.	Size dimorph.	Bright genitalia	Female ornaments
Presbytis aurata	98.41	9	1	0	1	1	-9	-9	-9	0	0	0
Presbytis cristata	106	32	1	0	1	0	1	0	1	0	0	1
Presbytis entellus	61.96	19	1	0	1	1	1	0	1	1	0	0
Presbytis francoisi	-9	-9	1	0	1	1	1	0	1	1	0	0
Presbytis frontata	-9	-9	1	0	1	1	1	0	1	0	0	0
Presbytis geei	94.19	9	1	0	1	1	1	0	1	1	0	0
Presbytis johnii	81.08	9	1	0	1	0	1	0	1	0	0	0
Presbytis melalophos	98.51	14	1	0	1	0	1	0	1	0	0	0
Presbytis obscura	78.31	10	1	0	1	1	1	0	1	1	0	0
Presbytis phayrei	85.62	-9	1	0	1	0	1	0	1	1	0	0
Presbytis pileatus	-9	-9	1	0	1	0	1	0	1	1	0	0
Presbytis potenziani	98.46	-9	1	0	1	-9	0	0	1	0	0	0
Presbytis rubicunda	100	-9	1	0	1	0	1	0	1	0	0	0
Presbytis vetulus	-9	-9	1	0	1	0	1	0	1	1	0	0
Procolobus verus	94.74	-9	1	0	0	1	1	0	1	0	0	0
Propithecus diadema	100	-9	1	0	0	-9	0	0	1	0	0	0
Propithecus verreauxi	94.59	6.5	1	0	0	1	1	0	0	0	0	0
Pygathrix avunculus	-9	-9	1	0	1	1	-9	-9	-9	0	0	0
Pygathrix nemaeus	75.23	-9	1	1	1	1	1	-9	1	1	1	0
Pygathrix roxellana	26.67	-9	1	1	1	1	1	-9	1	1	0	0
Saguinus bicolor	100	-9	1	0	0	1	-9	-9	-9	0	0	0
Saguinus fuscicollis	88.09	5	1	0	0	1	1	0	1	1	0	0
Saguinus imperator	100	-9	1	0	0	1	1	0	1	0	0	0
Saguinus labiatus	100	4	1	0	0	1	1	0	1	0	0	0
Saguinus leucopus	100	-9	1	0	0	1	1	0	1	0	0	0
Saguinus midas	88.33	-9	1	0	0	1	1	0	1	1	0	0
Saguinus mystax	100	5	1	0	0	1	1	0	1	0	1	0
Saguinus nigricollis	97.87	-9	1	0	0	1	0	0	1	0	0	0
Saguinus oedipus	113.33	6.4	1	0	0	1	1	0	1	0	0	0
Saimiri oerstedii	77.33	23	1	0	0	1	1	0	1	1	0	0
Saimiri sciureus	77.33	40.3	1	0	0	1	1	0	1	1	0	0
Simias concolor	81.14	-9	1	0	0	0	0	-9	1	1	0	0
Theropithecus gelada	66.36	-9	1	1	1	0	1	1	1	1	0	1
Varecia variegata	86.11	3	1	0	0	-9	0	0	1	1	0	0

Appendix 1.2 (cont): Ecological and behavioural variables for diurnal primates

Species	Male B.	Female B.	Natal B.	M. Crown	Cheek	Chest	Back	Out Leg	Rump	F. Crown	F Cheek	F Chest	F Back	F Out leg	F Rump	N. Crown	N Chest	N. Back	N. Out. Leg	N. Rump	M. Total	F. Total	N. Total
Allenopithecus nigroviridis	1	1	1	6	6.5	29	7	9	8 5	5	9.5	23	6.5	6	8.5	-9	-9	-9	-9	-9	66	58.5	-9
Alouatta belzebul	2	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Alouatta caraya	2	1	3	4	3	7.5	3	3.5	3.5	16.5	15	15.5	25.5	9.5	20	-9	-9	-9	-9	-9	24.5	102	-9
Alouatta fusca	1	2	3	5.5	6	5.5	10	6	6	16.5	15	15.5	25.5	9.5	20	-9	-9	-9	-9	-9	39	102	-9
Alouatta palliata	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Alouatta seniculus	3	3	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Alouatta villosa	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Ateles belzebuth	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Ateles fusciceps	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Ateles geoffroyi	1	1	3	4	8.5	10.5	6.5	3.5	5	3.5	6	7	4	3	5.5	-9	-9	-9	-9	-9	38	29	-9
Ateles paniscus	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Brachyteles arachnoides	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cacajao calvus	3	3	1	18	14.5	10.5	27.5	18	27	11.5	15.5	13.5	34	25.5	28.4	-9	-9	-9	-9	-9	115.5	128.4	-9
Cacajao melanocephalus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Callicebus moloch	2	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Callicebus personatus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Callicebus torquatus	3	3	1	4.5	5.5	8	5	5	5	3.5	4.5	11.5	5	8	4.5	-9	-9	-9	-9	-9	33	37	-9
Callimico goeldii	2	2	2	3	3.5	4	3	5	8.5	4	8.5	10.5	6.5	5.5	6	-9	-9	-9	-9	-9	27	41	-9
Callithrix argentata	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Callithrix humeralifer	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Callithrix jacchus	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cebuella pygmaea	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cebus albifrons	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cebus apella	1	1	1	3	8.5	8	7	5.5	5	3	22.5	30	5.5	4.5	5	5.5	21.5	21.5	9.5	11	37	70.5	69
Cebus capucinus	1	1	1	11.5	12.5	21	1.5	3.5	2	18.5	21	12.5	3	3.5	3	21.5	12.5	2	5.5	5	52	61.5	46.5
Cebus olivaceus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercocebus albigena	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercocebus aterrimus	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercocebus atys	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercocebus galeritus	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercocebus torquatus	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus aethiops	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus ascanius	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9

Appendix 1.3: Brightness and reflectance measurements for diurnal primates
(-9 indicates a missing variable)

Species	Male B.	Female B.	Natal B	M. Crown	Cheek	Chest	Back	Out. Leg	Rump	F. Crown	F. Cheek	F. Chest	F. Back	F. Out leg	F. Rump	N. Crown	N. Chest	N. Back	N. Out. Leg	N. Rump	M. Total	F. Total	N. Total
Cercopithecus campbelli	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus cephus	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus diana	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus erythrogaster	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus erythrotis	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus hamlyni	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus lhoesti	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus mitis	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus mona	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus neglectus	3	3	1	4.5	9.5	5.5	11.5	26	13.5	12.5	10	8.5	12	10	19	8	33.5	8	19	13	70.5	72	81.5
Cercopithecus nictitans	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus petaurista	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Cercopithecus pogonias	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Chiropotes albinasus	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Chiropotes satanas	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Colobus angolensis	2	2	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Colobus badius	3	3	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Colobus guereza	3	3	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Colobus polykomos	3	3	3	3.5	40	4	4	23	5	4.5	35.5	4.5	5	16.5	5	3.5	5.5	3.5	14.5	4	79.5	71	31
Colobus satanus	2	2	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Colobus vellerosus	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Erythrocebus patas	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Gorilla gorilla	2	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Hapalemur griseus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Hapalemur simus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Hylobates agilis	2	2	2	2.5	7.5	3	3.5	3.5	5	4	13	3.5	6	3	4.5	3	4	2.5	5.5	5	25	34	20
Hylobates concolor	1	2	2	2	4.5	3	2	3.5	3.5	15	17	14.5	16	18.5	14	12	11	14	23.5	5.5	18.5	95	66
Hylobates hoolock	3	1	2	20	7.5	4.5	10.5	16.5	11	20	7.5	4.5	10.5	16.5	11	-9	-9	-9	-9	-9	70	70	-9
Hylobates klossi	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Hylobates lar	2	2	2	2.5	19	5	5.5	5	6	16.5	27	21.5	20.5	17	13.5	8	6	9	11.5	18	43	116	52.5
Hylobates moloch	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Hylobates muelleri	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Hylobates pileatus	2	2	2	2.5	15.5	3.5	3.5	4	35.5	4	35.5	18	3	6.5	4	10.5	32	20.5	26	29	64.5	71	118

Appendix 1.3 (cont): Brightness and reflectance measurements for diurnal primates
(-9 indicates a missing variable)

Species	Male B.	Female B.	Natal B	M. Crown	Cheek	Chest	Back	Out Leg	Rump	F. Crown	F. Cheek	F. Chest	F. Back	F. Out. leg	F. Rump	N. Crown	N. Chest	N. Back	N. Out Leg	N. Rump	M. Total	F. Total	N. Total
Hylobates syndactylus	1	1	1	1.5	2.5	4	4	3.5	4	2.5	8.5	3	3.5	3.5	3	-9	-9	-9	-9	-9	19.5	24	-9
Indri indri	3	3	1	2	6.5	9	2.5	4	38	3	11	4	2.5	5	46.5	3.5	5	3	3	20.5	62	72	35
Lagothrix flavicauda	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Lagothrix lagothricha	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Lemur catta	3	3	1	5	34.5	50.5	12.5	16.5	13.5	7	37.5	56	15.5	14	15.5	3.5	5	3	3	20.5	132.5	136.5	35
Leontopithecus rosalia	3	3	1	27	43.5	19	33.5	14.5	25.5	14	40.5	15.5	27	10.5	25	-9	-9	-9	-9	-9	163	132.5	-9
Macaca arctoides	2	2	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Macaca assamensis	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Macaca cyclopis	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Macaca fascicularis	1	1	1	10.5	6.5	18	7.5	13.5	6	9	16.5	7.5	9	14	8	7.5	25	8	23.5	16	62	64	80
Macaca fuscata	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Macaca mulatta	1	1	1	9.5	12	10	9.5	17	12	9	10.5	7	8.5	12	11	-9	-9	-9	-9	-9	70	58	-9
Macaca nemestrina	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Macaca nigra	1	1	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Macaca radiata	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Macaca silenus	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Macaca sinica	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Macaca sylvanus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Mandrillus leucophaeus	3	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Mandrillus sphinx	3	2	2	4.5	22.5	4	4.5	4.5	18.5	7.5	14	24	5	12	6	-9	-9	-9	-9	-9	58.5	68.5	-9
Miopithecus talapoin	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Nasalis larvatus	2	2	3	7.5	19	31	9.5	16	17.5	-9	-9	-9	-9	-9	-9	12	29.5	14.5	17.5	15.5	100.5	-9	89
Pan paniscus	1	1	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Pan troglodytes	1	1	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Papio anubis	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Papio cynocephalus	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Papio hamadryas	1	1	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Papio papio	2	2	2	6	14.5	10.5	5	8.5	13.5	-9	-9	-9	-9	-9	-9	8	11	7.5	16.5	21	58	-9.	64
Papio ursinus	1	1	2	4.5	7.5	12.5	4.5	9	9.5	8.5	14.5	9	6.5	6	12	3.5	7.5	2.5	5.5	5	47.5	56.5	24
Petterus coronatus	2	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Petterus fulvus	2	1	1	1.5	6	25.5	7	12.5	8.5	2	3	25	6.5	11.5	8	-9	-9	-9	-9	-9	61	56	-9
Petterus macaco	1	2	2	1.5	3	6	2.5	4.5	2	8	25.5	24.5	11.5	24	17.5	-9	-9	-9	-9	-9	19.5	111	-9
Petterus mongoz	1	2	2	4.5	28.5	21	5	17	12	9.5	27.5	29	8.5	16.5	9.5	-9	-9	-9	-9	-9	88	100.5	-9

Appendix 1.3 (cont): Brightness and reflectance measurements for diurnal primates
(-9 indicates a missing variable)

Species	Male B.	Female B.	Natal B.	M. Crown	Cheek	Chest	Back	Out. Leg	Rump	F. Crown	F. Cheek	F. Chest	F. Back	F. Out leg	F. Rump	N. Crown	N. Chest	N. Back	N. Out. Leg	N. Rump	M. Total	F. Total	N. Total
Petterus rubriventer	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Pithecia monachus	1	2	1	6	7.5	10	5.5	4	6	7	11	8	6	5	5.5	10.5	21.5	5	5	5.5	39	42.5	47.5
Pithecia pithecia	2	2	2	31	21.5	6.5	4.5	4	5	5.5	8.5	12	3.5	6	5.5	-9	-9	-9	-9	-9	72.5	41	-9
Pongo pygmaeus	3	3	3	5.5	7.5	4.5	5	4.5	5	4.5	7.5	4	4	5	5	-9	-9	-9	-9	-9	32	30	-9
Presbytis aurata	2	2	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Presbytis cristata	2	2	3	6	7.5	14	5.5	7.5	4.5	6.5	6.5	7	5.5	6.5	5.5	33.5	23.5	22.5	40.5	25	45	37.5	145
Presbytis entellus	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Presbytis francoisi	2	2	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Presbytis frontata	2	2	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Presbytis geei	3	3	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Presbytis johnii	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Presbytis melalophos	2	2	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Presbytis obscura	1	1	3	7.5	9.5	24	9.5	7.5	7	16	5.5	17	11.5	9.5	10.5	16.5	17	10	27.5	17	65	70	88
Presbytis phayrei	1	1	3	7.5	6.5	15.5	6.5	11	6.5	7.5	10	15	6	8	6	17.5	22.5	13	12.5	15	53.5	52.5	80.5
Presbytis pileatus	1	1	3	8.5	10.5	13	7	18	12.5	8	13.5	17	6.5	15	16	18	30	21	26.5	14	69.5	76	109.5
Presbytis potenziani	2	2	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Presbytis rubicunda	3	3	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Presbytis vetulus	1	1	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Procolobus verus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Propithecus diadema	3	3	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Propithecus verreauxi	3	3	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Pygathrix avunculus	3	3	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Pygathrix nemaeus	3	3	2	8	28	9.5	12	4	50	4.5	13	7.5	9	4.5	26.5	4.5	18.5	10.5	4.5	36.5	111.5	65	74.5
Pygathrix roxellana	3	2	2	6	11	24	13.5	11	31.5	19.5	24	23.5	11.5	22.5	8.5	9	27	18	17	23	97	109.5	94
Saguinus bicolor	3	3	3	27.5	2.5	42	61	12.5	13	38	3.5	45	42	12.5	10.5	-9	-9	-9	-9	-9	158.5	151.5	-9
Saguinus fuscicollis	3	3	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Saguinus imperator	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Saguinus labiatus	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Saguinus leucopus	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Saguinus midas	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Saguinus mystax	1	1	1	4	16.5	3.5	2.5	4	4.5	4.5	20.5	16	4	5	6.5	-9	-9	-9	-9	-9	35	56.5	-9
Saguinus nigricollis	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Saguinus oedipus	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9

Appendix 1.3 (cont): Brightness and reflectance measurements for diurnal primates
(-9 indicates a missing variable)

Species	Male B.	Female B.	Natal B.	M. Crown	Cheek	Chest	Back	Out Leg	Rump	F. Crown	F. Cheek	F. Chest	F. Back	F. Out leg	F. Rump	N. Crown	N. Chest	N. Back	N. Out. Leg	N. Rump	M. Total	F. Total	N. Total
Saimiri oerstedii	2	2	2	5	30.5	32 5	7.5	15	10	5	31	34	9.5	14 5	10	-9	-9	-9	-9	-9	100.5	104	-9
Saimiri sciureus	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Simias concolor	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Theropithecus gelada	3	3	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9
Varecia variegata	3	3	3	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9

Appendix 1.3 (cont): Brightness and reflectance measurements for diurnal primates

(-9 indicates a missing variable)

Species	% male weight	Av. group size	Size dimorphism	Activity	Sex. dichromatism	Natal colouration	Male grouping	mon/pol	arb/terr	Male dominance
Allocebus trichotis	100	-9	0	0	0	0	-9	-9	0	1
Aotus trivirgatus	108.7	4	0	0	0	0	-9	0	0	1
Arctocebus calabarensis	96.87	-9	0	0	0	0	-9	-9	0	1
Avahi laniger	100	2	0	0	0	0	-9	0	0	1
Cheirogaleus major	100	-9	0	0	0	0	-9	-9	-9	1
Cheirogaleus medius	100	6	0	0	0	0	-9	-9	-9	1
Daubentonia madagascariensis	100	2	0	0	0	0	-9	-9	0	1
Euoticus elegantulus	96.55	-9	0	0	0	0	0	-9	0	1
Euoticus inustus	-9	-9	0	0	0	0	0	1	0	1
Galago alleni	85.18	-9	1	0	0	0	-9	1	0	1
Galago senegalensis	90.48	3	1	0	0	0	-9	1	1	1
Galagoides demidoff	98.41	-9	0	0	0	0	-9	1	0	1
Lepilemur mustelinus	104.92	2	0	0	0	0	-9	0	0	1
Loris tardigradus	89.65	-9	1	0	0	0	-9	-9	0	1
Microcebus murinus	100	2	0	0	0	0	-9	-9	0	0
Microcebus rufus	100	-9	0	0	0	0	-9	-9	0	1
Mirza coquereli	100	-9	0	0	0	0	0	-9	0	1
Nycticebus coucang	92.31	-9	0	0	0	0	-9	-9	0	1
Nycticebus pygmaeus	100	-9	0	0	0	0	-9	-9	0	1
Otolemur crassicaudatus	100	-9	0	0	0	0	-9	1	0	1
Otolemur garnettii	100	-9	0	0	0	0	-9	1	0	1
Perodicticus potto	105.89	-9	0	0	0	0	-9	1	0	1
Phaner furcifer	90.91	-9	1	0	0	0	-9	0	0	0
Tarsius bancanus	92.31	-9	0	0	0	0	-9	0	0	1
Tarsius spectrum	100	2	0	0	0	0	-9	0	0	1
Tarsius syrichta	92.31	2	0	0	0	0	-9	-9	0	1

Appendix 1.4: Ecological and behavioural variables for nocturnal primates
(-9 indicates a missing variable)

Species	Male brightness	Female brightness	Natal brightness	M. Crown	M. Cheek	M. Chest	M Back	M Out. leg	M Rump	M. Total	F Crown	F Cheek	F. Chest	F. Back	F. Out leg	F Rump	F. Total	N Crown	N. Chest	N. Back	N. Out. leg	N. Rump	N. Total	Activity
Allocebus trichotis	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Aotus trivirgatus	1	1	1	3.5	-9	31.5	8	9.5	8.5	-9	6	-9	31	8.5	12	12	-9	-9	-9	-9	-9	-9	-9	0
Arctocebus calabarensis	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Avahi laniger	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Cheirogaleus major	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Cheirogaleus medius	1	1	1	14.5	-9	42	15.5	17	16	-9	11	-9	41.5	12	19	17.5	-9	12	32.5	27	20.5	16.5	108.5	0
Daubentonia	1	1	1	5	5.5	16.5	19	3.5	2.5	52	5	5.5	16.5	19	3.5	2.5	52	-9	-9	-9	-9	-9	-9	0
Euoticus elegantulus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Euoticus inustus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Galago alleni	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Galago senegalensis	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Galagoides demidoff	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Lepilemur mustelinus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Loris tardigradus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Microcebus murinus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Microcebus rufus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Mirza coquereli	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Nycticebus coucang	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Nycticebus pygmaeus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Otolemur crassicaudatus	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Otolemur garnettii	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Perodicticus potto	2	2	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	4	22	5	9.5	8.5	49	0
Phaner furcifer	2	2	2	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Tarsius bancanus	1	1	1	10	-9	13.5	8.5	14	13.5	-9	10	-9	12	10	13.5	18.5	-9	-9	-9	-9	-9	-9	-9	0
Tarsius spectrum	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0
Tarsius syrichta	1	1	1	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	-9	0

Appendix 1.5: Brightness and reflectance measurements for nocturnal primates (-9 is missing variable)

SPECIES	GENITALIA ORNAMENT/COLOUR *	SEX
Allenopithecus nigroviridis	Light blue scrotum	M
Callithrix sp.	White hairless scrotum	M
Cebuella pygmaea	Bright coloured glands under scrotal skin	M
Cercopithecus diana	Orange genitalia	M/F
Cercopithecus nicititans	Blue scrotum	M
Cercopithicus aethiops	Blue scrotum, red penis	M
Chiropotes albinasus	Pink scrotum	M
Chiropotes satanus	Pink scrotum	M
Erythrocebus patas	Blue scrotum	M
Hylobates moloch	Black genital spot	M/F
Hylobates pileatus	White pubic tuft and genital tassle	M
Hylobates syndactylus	Black tuft	M
Lagothrix flavicauda	Yellow genital tuft	M
Pan troglodytes	Pink bald rump	M/F
Papio leucophaeus	As above more metallic, blue ischial callosities	M
Papio sphinx	Lilac scrotum, red genitalia, scarlet pubic hair	M
Pithecia hirsuta	Bald, pink genitalia	M
Pygathrix nemaeus	White spots on rump patch	M
Saguinus mystax	White genito anal patch	M/F

* = Does not refer to female oestral cyclical swelling/reddening of genitalia

Appendix 1.6: Species displaying bright genitalia

SPECIES	FEMALE ORNAMENTS NOT IN MALE
Cebus albifrons	Light coloured superciliary brush of hair
Cebus capucinus	Brown tuft on head
Eulemur mongoz	White cheeks and ear tufts
Hylobates agilis	Separate white eyebrows
Pithecia monachus	Light oblique nasal streaks
Presbytis cristatus	Patch of pale hairs beneath callosities
Theropithecus gelada	Pink chest patch surrounded by caruncles

Appendix 1.7: Ornamentations present in females

Species	Natal Pelage	Dichromatic Pelage	
		Male pelage	Female pelage
Eulemur coronatus	as female	orange crown, dark grey cap, orange cheeks orange/brown back and legs, dark tail	orange crown, dark grey cap, grey pelage grey tail
Eulemur mongoz	as female	brown/grey pelage, red neck, cheeks and throat	greyer pelage, white cheeks and throat
Eulemur fulvus rufus	as male	grey, black crown	reddish pelage, grey crown
Eulemur macaco	dark grey	completely black	red/brown, white cheek tufts
Eulemur rubriventer	as female	red/brown, red venter, red cheek whiskers	red/brown, lighter venter, white cheek whiskers
Callimico goeldi	brown/black	None, Black pelage	
Pithecia pithecia	similar to female	black, white mask surrounding muzzle	light brown/grey flecked with gold, gold chest
Alouatta caraya	as female	black	straw coloured pelage
Alouatta fusca	as female	dark brown	olive/brown
Ateles geoffroyi	black, pink face	None, golden, red, buff or dark brown with black crown, hands and feet	
Pygathrix nemaeus	black face, pale white orbital stripe	two white rump patches, red to knee, grey chest and back, red collar, white face	as male, white triangular rump patch and tail
Pygathrix roxellana	paler	None, orange rump, face hands and feet, blue around eyes, grey/brown pelage and mane secondary sexual character – blue warts around lip	
Pygathrix avunculus	paler	None, black, yellow white underparts	
Nasalis larvatus	black, blue face	None, orange, white chest and limbs	
Presbytis *aurata*	orange	None, black	
Presbytis comata	white, dark stripe down back to tail tip	None	
Presbytis frontata	white, dark stripe down back to tail tip	None	
Presbytis melalaphos	white, dark stripe down back to tail tip	None, vary geographically, grey/black/red or brown	
Presbytis rubicunda	white, dark stripe down back to tail tip	None	
Presbytis cristata	bright orange, pale eye rings	None, grey/silver	
Presbytis francoisi	bright orange, pale eye rings	None, black with white cheeks	
Presbytis geei	white	None	
Presbytisjohnii	reddish brown	black	
Presbytis vetulus	pale grey	None, grey/brown	
Presbytis obscura	bright orange, white spectacled eye	None, black/brown white eyes and lips	

Appendix 1.8: Descriptions of species displaying a natal pelage or sexual dichromatism

Species	Natal Pelage	Dichromatic Pelage	
		Male pelage	Female pelage
Presbytis phayrei	bright orange, pale eye rings	None	
Presbytis pileatus	bright orange, no eye rings	None	
Presbytis potenziani	bright orange, pale eye rings	None	
Presbytis entellus	dark brown	None, pale grey/fawn	
Colobus angolensis	white	None, black, white mantle and tail tip, white surrounding face	
Colobus guereza	white	None, black, white mantle and tail tip, white surrounding face	
Colobus satanas	white	None, black, white mantle and tail tip, white surrounding face	
Colobus polykomos	white	None, black, white mantle and tail tip, white surrounding face	
Macaca arctoides	white	None, dark brown, red face	
Macaca radiata	dark coat, pale skin	None, grey/brown	
Macaca fuscata	black, pink face and hands	None, grey/brown	
Macaca fascicularis	dark brown	None, grey/brown	
Macaca silenus	brown/grey	None, black grey ruff	
Mandrillus sphinx	as female, lighter	gold, flecked brown pelage, yellow cape, beard and whiskers, red and blue nose, violet/red and blue genitalia	brown pelage, red/orange rump
Papio papio	black, brown, pink face	None, red rufous	
Papio anubis	black, brown, pink face	None, dark olive/grey	
Papio cyanocephalus	black, brown, pink face	None, yellow rufous	
Papio ursinus	black, brown, pink face	None, dark brown to almost black	
Papio hamadryas	black, brown, pink face	silver grey, silver cape and whiskers	pale olive brown
Theropithecus gelada	dark, smoky brown	yellow brown cape and mane, white Chest, eyelids and lips, brown pelage	brown pelage, large chest patches (red in oestrus)
Cercopithecus neglectus	orange, brown flecked	None, orange eyebrow patch, brown flecked pelage, white beard, pale blue muzzle	
Erythrocebus patas	pale with black triangle on nose	None, orange/grey pelage, white venter and inner limbs and cheeks	
Hylobates pileatus	silver, white face ring, dark chest patch	black, white pubic tuft, hands, feet, brow	grey, black crown and throat
Hylobates concolor	fawn	black	cream/buff
Hylobates hoolock	fawn	black	golden brown
Gorilla gorilla	as female, white tuft	black, silver back	black

Appendix 1.8 (cont): Descriptions of species displaying a natal pelage or sexual dichromatism

Two-way table 1
Hypothesis 1 (nocturnal species included)

no. species Natal colouration		Sexual dichromatism presence		absence		Total S
presence	*a*	10	*b*	38	*a* + *b*	48
absence	*c*	8	*d*	100	*c* + *d*	108
Totals	*a* + *c*	18	*b* + *d*	138	*n*	= 156

Two-way table 2
Hypothesis 2 (nocturnal species included)

no. species sexual dimorphism		Sexual dichromatism presence		absence		Total S
presence	*a*	10	*b*	70	*a* + *b*	80
absence	*c*	8	*d*	68	*c* + *d*	76
Totals	*a* + *c*	18	*b* + *d*	138	*n*	= 156

Two-way table 3
Hypothesis 3 (nocturnal species included)

no. species Single male grouping		Sexual dichromatism presence		absence		Total S
presence	*a*	3	*b*	36	*a* + *b*	39
absence	*c*	15	*d*	102	*c* + *d*	117
Totals	*a* + *c*	18	*b* + *d*	138	*n*	= 156

Two-way table 4
Hypothesis 4 (nocturnal species included)

no. species Multimale grouping		Sexual dichromatism presence		absence		Total S
presence	*a*	7	*b*	68	*a* + *b*	75
absence	*c*	11	*d*	70	*c* + *d*	81
Totals	*a* + *c*	18	*b* + *d*	138	*n*	= 156

Two-way table 5
Hypothesis 5 (nocturnal species included).

no. species Sexual size dimorphism		Natal colouration presence		absence		Total S.
presence	*a*	33	*b*	47	*a* + *b*	80
absence	*c*	15	*d*	61	*c* + *d*	76
Totals	*a* + *c*	48	*b* + *d*	108	*n*	= 156

Appendix 2.1: Two-way tables used in the test of independence

Two-way table 6
Hypothesis 6 (nocturnal species included)

no. species Multimale grouping		Natal colouration presence		absence		Total S
presence	*a*	21	*b*	54	*a* + *b*	75
absence	*c*	27	*d*	54	*c* + *d*	81
Totals	*a* + *c*	48	*b* + *d*	108	*n*	= 156

Two-way table 7
Hypothesis 7 (nocturnal species included)

no. species Single male grouping		Natal colouration presence		absence		Total S
presence	*a*	12	*b*	27	*a* + *b*	39
absence	*c*	36	*d*	81	*c* + *d*	117
Totals	*a* + *c*	48	*b* + *d*	108	*n*	= 156

Two-way table 8
Hypothesis 1 (nocturnal species excluded)

no. species Natal colouration		Sexual dichromatism presence		absence		Total S
presence	*a*	10	*b*	38	*a* + *b*	48
absence	*c*	8	*d*	74	*c* + *d*	82
Totals	*a* + *c*	18	*b* + *d*	112	*n*	= 130

Two-way table 9
Hypothesis 2 (nocturnal species excluded)

no. species Sexual size dimorphism		Sexual dichromatism presence		absence		Total S
presence	*a*	10	*b*	70	*a* + *b*	80
absence	*c*	8	*d*	42	*c* + *d*	50
Totals	*a* + *c*	18	*b* + *d*	112	*n*	= 130

Two-way table 10
Hypothesis 3 (nocturnal species excluded)

no. species Single male grouping		Sexual dichromatism presence		absence		Total S.
presence	*a*	3	*b*	36	*a* + *b*	39
absence	*c*	15	*d*	76	*c* + *d*	91
Totals	*a* + *c*	18	*b* + *d*	112	*n*	= 130

Appendix 2.1 (cont): Two-way tables used in the test of independence

Two-way table 11
Hypothesis 4 (nocturnal species excluded)

no. species Multimale grouping		Sexual dichromatism presence		absence	Total S
presence	*a*	7	*b*	68	*a* + *b* 75
absence	*c*	11	*d*	44	*c* + *d* 55
Totals	*a* + *c*	18	*b* + *d*	112	*n* = 130

Two-way table 12
Hypothesis 5 (nocturnal species excluded)

no. species Sexual size dimorphism		Natal colouration presence		absence	Total S
presence	*a*	33	*b*	47	*a* + *b* 80
absence	*c*	15	*d*	35	*c* + *d* 50
Totals	*a* + *c*	48	*b* + *d*	82	*n* = 130

Two-way table 13
Hypothesis 6 (nocturnal species excluded)

no. species Multimale grouping		Natal colouration presence		absence	Total S
presence	*a*	21	*b*	54	*a* + *b* 75
absence	*c*	27	*d*	28	*c* + *d* 55
Totals	*a* + *c*	48	*b* + *d*	82	*n* = 130

Two-way table 14
Hypothesis 7 (nocturnal species excluded)

no. species Single male grouping		Natal colouration presence		absence	Total S
presence	*a*	12	*b*	27	*a* + *b* 39
absence	*c*	36	*d*	55	*c* + *d* 91
Totals	*a* + *c*	48	*b* + *d*	82	*n* = 130

Appendix 2.1 (cont): Two-way tables used in the test of independence

Code	Female brightness	Bright genitalia	Variance	Height	Subtaxa	Female brightness at node	Genitalia at node
BBBAABAAABAAAB	0	1	1.36	0.68	2	3	-9
BBBAABAAABAABA	0	1	2.47	1.77	2	3	-9
BBBAAAAAAAAABA	-0.4131	1	1.465	0.89	2	1.30375	-9
BBBAAAAAAAAA	-0.21574	1	3.238	2.13	2	1.25536	-9
BBBAABAAA	-0.90184	1	3.801	3	2	2.38772	-9
BBBABBBBA	-0.39666	1	5.187	3.9	10	1.67924	-9
BBBABAAA	-1.56174	1	0.41	0.23	2	2.56098	-9
AAAAAB	0.12684	1	15.54	10.43	2	1.66441	-9
BBAAAA	-0.03847	1	17.639	13.41	2	2.12284	-9
BBBAAB	-0.51755	1	8.4	5.2	2	1.92857	-9
ABBAA	0	1	11.96	5.98	2	1	-9
BBAAB	0	1	28	14	2	1	-9
ABAA	0	1	1.78	0.89	2	1	-9
ABAE	0	1	1.12	0.56	2	1	-9
ABA	0	1	3.44	1.86	2	1	-9

df	Sample mean	Pop. Mean	*t*-value	Prob. (2 tail)
14	-0.261	0	-.2.227	0.0429

Appendix 2.2: A typical output from CAIC, and the statistical table using BRUNCH (one continuous and one categorical variable, -9 indicates a missing variable)

Code	Av. group size	M. Crown	M. Cheek	M. Chest	M. Back	M. Out Leg	M. Rump	M. Total	Variance	Height	Subtaxa	Av. group size at node	M. Crown at node	M. Cheek at node	M. Chest at node	M. Back at node	M. Out Leg at node	M.Rump at node	M. Total at node
BBBAAAAAAAAAB	4.69334	-0.5522	3.03687	-4.4173	1.10432	1.93255	3.31295	4.41726	3.28	1.64	2	31.25	10	9.25	14	8.5	15.25	9	66
BBBBAAAAAAA	0.29981	0	-8.6196	-1.4991	-1.4991	-1.1243	-0.74953	-13.492	1.78	0.89	2	4.2	2.5	13.25	4	4.5	4.25	5.5	34
BBBABBBBA	7.87726	-0.5371	-0.7161	-3.5806	-1.4322	0	-0.89514	-7.1612	7.8	3.9	2	21	6.75	8.5	19	7.5	7.5	5.75	55
AAAAABAB	0.34259	0	-1.0278	-6.6806	-1.5417	-2.74075	-2.22686	-14.218	8.52	4.26	2	9.5	1.5	4.5	15.75	4.75	8.5	5.25	40.25
BBBBAAAA	0.33903	0	-1.5256	0.339	0.67806	0.16952	-20	-20.681	2.175	1.31	2	4.00115	2.5	14.14483	3.80115	4.1023	4.15057	17.43104	46.12989
AAAAABA	1.94363	-0.7775	-6.2196	-1.3605	-0.0648	-2.20278	-1.74927	-12.374	14.89	8.51	2	6.28643	2.78543	14.78341	17.9995	4.85712	12.14204	8.14221	60.70971
BBAAAAA	0	-4.4412	-5.2136	-2.993	-5.9859	-2.0275	-4.05499	-24.716	26.82	13.41	2	5	15.5	30	11.25	18	9.25	15	99
BBAAABA	0.33445	1.42141	0.6689	2.1739	-0.9197	-0.33445	-0.50168	2.50838	35.76	17.88	2	14	7.25	10.5	14.5	4.25	4.5	3.5	44.5
BBBAAAB	9.17248	0	-4.1318	2.3413	0	1.23952	-2.47905	-3.03	13.18	6.59	2	30.55	4.5	15	8.25	4.5	6.75	14	53
BBBABBB	0.39436	-0.2958	-4.1408	-4.7323	-0.7887	-3.35207	-4.63375	-17.943	6.43	4.19	2	20.65163	7.01128	12.15786	23.1804	8.19673	10.46112	9.84331	70.85071
BBAAAA	0.49053	-2.7871	-5.9086	-1.6165	-3.3445	-0.94761	-1.44928	-16.054	20.115	13.41	2	5.73333	11.33333	21.16667	8.83333	13	7.83333	12.83333	75
BBAAAB	1.56528	-0.3913	3.47839	3.1306	0.56524	1.82616	1.13048	9.7395	33.06	21	2	17.28312	6.42922	17.79583	21.06624	5.43557	8.33031	5.87114	64.92831
BBABAA	0	7.45025	4.17214	-1.043	-0.298	0	-0.29801	9.98333	11.26	5.63	2	3	18.5	14.5	8.25	5	4	5.5	55.75
BBBAAA	0.21276	1.67166	-1.7477	1.7477	1.21575	2.58348	-1.51969	3.9512	10.825	7.47	2	30.81998	6.62125	12.78233	10.46767	6.04273	10.02829	12.07159	58.01385
BBBBAA	0.22159	-4.8404	1.83793	-0.1933	-1.7696	-3.4158	1.7788	-6.6024	13.071	6.93	2	3.62476	10.72182	11.02297	4.12948	7.10806	9.95256	14.40962	57.3445
AAAAA	2.2235	0.45961	4.09199	6.7452	1.58621	0.90445	1.11196	14.8994	23.216	14.04	2	10.521	3.66074	22.57646	30.84542	7.87799	13.86454	10.25989	89.08504
BBAAA	1.78004	-0.7558	-0.5195	1.8853	-1.1658	0.07659	-1.073	-1.5522	42.101	32.19	2	12.11168	8.62504	19.30513	15.58894	8.82256	8.10779	8.98847	69.43792
BBABA	4.6641	-0.1372	0	0.6173	6.17308	3.84103	5.89872	16.393	13.285	8.05	2	9.69891	18.30297	14.5	9.13662	13.8662	9.51675	13.97215	79.29469
BBABB	1.64317	0	1.00416	0.5477	0.63901	0	0.27386	2.46475	30	15	2	12.5	4	5.75	9	4.75	3.5	4.25	31.25
BBBAA	7.66023	0.16513	1.66982	-4.9258	-0.2544	0.27332	0.94932	-2.1227	14.155	9.53	2	21.40365	6.41827	10.72971	16.52272	6.3555	9.69232	10.90465	60.62316
BBBBA	0.12509	-1.9504	-1.9492	0.0686	-0.4506	-1.33137	-2.10017	-7.7132	10.988	7.83	3	3.70452	6.10704	7.10423	3.83791	5.06439	6.64479	8.96075	37.71912
BBAB	0.48308	-2.4667	-1.509	-0.0236	-1.5722	-1.03765	-1.67668	-8.2858	33.622	23	2	11.20868	10.59375	9.7838	9.06298	8.95262	6.27376	8.73197	53.39888
BBBA	0.16981	-0.1339	-0.3225	-1.5033	-0.4158	-0.1736	0.23965	-2.3094	19.613	14.38	2	21.09831	6.65905	11.30959	19.22598	7.1031	10.00448	10.47371	64.77591
AAA	1.33985	0.29586	2.86398	3.8917	0.95808	1.75734	-4.94184	4.82514	31.509	20	2	7.77382	3.05413	16.70424	22.86599	5.91358	10.26134	20.39246	79.19175
BBA	0.17079	-0.3724	1.80082	1.2343	-0.0246	0.34688	0.04851	3.03355	27.955	32.19	2	11.77541	9.35819	15.75941	13.15869	8.87099	7.4248	8.89295	63.46503
BBB	2.75811	0.08753	0.66684	2.4401	0.32328	0.53274	0.23991	4.29036	39.771	27.5	2	13.29152	6.4113	9.42211	12.31941	6.18808	8.49656	9.79465	52.63211
BB	0.24698	-0.4801	-1.0324	-0.1367	-0.4371	0.1746	0.14689	-1.7647	37.682	40.5	2	12.37263	8.19736	13.26306	12.82809	7.81415	7.84698	9.24815	59.19779
@Root	0.54654	0.61124	-0.409	-1.193	0.22587	-0.28693	-1.32444	-2.3762	70.802	57.5	2	10.68407	6.30891	14.52657	16.51372	7.11632	8.73347	13.34002	66.53901

Appendix 2.3: Example of an output from CAIC using CRUNCH (two continuous variables, -9 indicates a missing variable)

Regression Summary
M. Rump vs. Av. group size

ANOVA Table
M. Rump vs. Av. group size

	DF	Sum of Squares	Mean Square	*F*-Value	*p*-Value
Regression	1	26.516	26.516	1.463	0.2373
Residual	26	471.099	18.119		
Total	27	497.615			

Regression Coefficients
M. Rump vs. Av. group size

	Coefficient	Std. Error	Std. Coeff.	*t*-Value	*p*-Value
Intercept	-2.011	0.994	-2.011	-2.024	0.0534
Av. group size	0.383	0.316	0.231	1.21	0.2373

Confidence Intervals
M. Rump vs. Av. group size

	Coefficient	95% Lower	95% Upper
Intercept	-2.011	-4.054	0.032
Av. group size	0.383	-0.267	1.032

Residual Statistics
M. Rump vs. Av. group size

# >= 0	19
# < 0	9
SS[e(i) - e(i-1)]	849.013
Durbin-Watson	1.802
Serial Autocorrelation	0.085

Regression Plot
Y = -2.011 + .383 * X; R^2 = .053

Appendix 2.4: Statistical results from CAIC output using CRUNCH (two continuous variables)

Lemur species	Name	Sex	crown	cheek	chest	back	out.leg	rump	Sample no.	*Strong.f1*	*Strong.f3*	*Lemuricola*	*Strongyloides*	Tot. bright.	Av. load	Av *Lemur.*	Av. *Strong.*	Mean Br.	*e* (eggs/g)	*h*	*asc*	*k*	*d*	*s*
Eulemur	Sorrel	M	3	8	18	6	15	8	80	0	0	0	0	58	7	1	0.25	9.67	100	0	100	0	0	0
fulvus rufus			3	8	18	6	15	8	76	0	0	4	0	58	7			9.67	0	0	200	0	0	0
			3	8	18	6	15	8	127	0	0	0	0	58	7			9.67	200	0	300	0	0	100
			3	8	18	6	15	8	40	0	1	0	1	58	7			9.67	0	0	400	0	0	400
	Rory	M	1	9	25	3	8	6	121	0	2	1	2	52	7.33	0.33	1	8.67	200	300	600	0	0	400
			1	9	25	3	8	6	123	0	0	0	0	52	7.33			8.67	0	200	100	0	0	500
			1	9	25	3	8	6	124	0	1	0	1	52	7.33			8.67	100	100	0	0	0	300
	Redoak	M	3	13	28	9	15	17	78	1	3	3	4	85	8.57	0.57	4.71	14.17	500	300	0	0	0	0
			3	13	28	9	15	17	81	0	15	0	15	85	8.57			14.17	700	0	200	200	0	0
			3	13	28	9	15	17	23	0	2	0	2	85	8.57			14.17	1900	800	100	0	0	500
			3	13	28	9	15	17	128	0	3	1	3	85	8.57			14.17	700	400	100	300	0	500
			3	13	28	9	15	17	129	0	3	0	3	85	8.57			14.17	500	0	400	200	0	500
			3	13	28	9	15	17	79	0	3	0	3	85	8.57			14.17	400	100	200	0	0	300
			3	13	28	9	15	17	126	0	2	0	2	85	8.57			14.17	1700	600	0	0	0	300
	Carmine	M	2	22	25	10	23	15	25	2	5	0	7	97	18	0	10.2	16.17	0	0	200	0	0	100
			2	22	25	10	23	15	26	0	5	0	5	97	18			16.17	100	100	300	0	0	600
			2	22	25	10	23	15	84	3	7	0	10	97	18			16.17	100	0	500	0	0	500
			2	22	25	10	23	15	3	0	8	0	8	97	18			16.17	300	300	400	0	0	1000
			2	22	25	10	23	15	41	1	20	0	21	97	18			16.17	300	400	900	0	0	900
	Redwood	F	3	8	23	7	14	17	60	4	0	0	4	72	9	0	3	12	400	400	400	0	0	0
			3	8	23	7	14	17	103	0	4	0	4	72	9			12	100	200	0	0	0	0
			3	8	23	7	14	17	75	0	0	0	0	72	9			12	500	500	0	0	0	400
			3	8	23	7	14	17	51	4	0	0	4	72	9			12	200	500	600	0	0	10
			3	8	23	7	14	17	116	3	0	0	3	72	9			12	150	400	0	0	0	0
	Strawberry	F	2	20	36	5	13	16	109	0	2	0	2	92	3.62	0.12	2	15.33	0	100	200	0	0	0
			2	20	36	5	13	16	108	0	0	0	0	92	3.62			15.33	0	0	200	0	0	200
			2	20	36	5	13	16	28	0	0	1	0	92	3.62			15.33	100	0	200	0	0	0
			2	20	36	5	13	16	69	0	0	0	0	92	3.62			15.33	0	0	0	0	0	0
			2	20	36	5	13	16	96	0	0	0	0	92	3.62			15.33	0	200	100	0	0	200
			2	20	36	5	13	16	91	0	2	0	2	92	3.62			15.33	0	0	300	0	0	0
			2	20	36	5	13	16	42	0	0	0	0	92	3.62			15.33	300	0	500	0	0	0
			2	20	36	5	13	16	120	0	0	0	0	92	3.62			15.33	0	0	600	0	0	0
	Rosella	F	7	8	27	8	10	17	22	0	0	2	0	77	6.25	0 5	0.75	12.83	300	0	600	0	0	300
			7	8	27	8	10	17	122	0	0	0	0	77	6.25			12 83	0	0	400	0	0	100
			7	8	27	8	10	17	83	0	0	0	0	77	6.25			12 83	0	0	200	200	0	300
			7	8	27	8	10	17	411	1	2	0	3	77	6.25			12.83	0	200	600	0	0	400
	Redbay	F	3	7	26	4	3	12	125	1	1	0	2	55	9	0	2	9.17	300	0	500	300	0	0

Appendix 3.1: Reflectance measurements and parasite loads

Lemur species	Name	Sex	crown	cheek	chest	back	out.leg	rump	Sample no	*Strong f1*	*Strong.f3*	*Lemuricola*	*Strongyloides*	Tot. bright.	Av. load	Av *Lemur.*	Av. *Strong.*	Mean Br.	*e* (eggs/g)	*h*	*asc*	*k*	*d*	*s*
Eulemur	Redlake	F	6	17	28	13	15	10	33	3	4	2	7	89	21.44	0.22	9.44	14.83	300	800	1800	0	300	800
fulvus rufus			6	17	28	13	15	10	86	1	2	0	3	89	21.44			14.83	300	700	1800	0	0	2400
			6	17	28	13	15	10	88	6	7	0	13	89	21.44			14.83	100	300	2100	0	0	1500
			6	17	28	13	15	10	85	11	7	0	18	89	21.44			14.83	0	100	0	0	0	300
			6	17	28	13	15	10	59	7	13	0	20	89	21.44			14.83	0	400	800	0	0	900
			6	17	28	13	15	10	29	2	7	0	9	89	21.44			14.83	0	100	300	0	0	500
			6	17	28	13	15	10	66	1	2	0	3	89	21.44			14.83	400	0	0	0	0	200
			6	17	28	13	15	10	104	1	2	0	3	89	21.44			14.83	0	0	400	0	0	1900
Lemur catta	Dory	F	6	50	66	6	21	30	73	1	40	0	41	179	50	0	14.25	29.83	800	0	400	0	0	2500
			6	50	66	6	21	30	61	0	4	0	6	179	50			29.83	600	100	2200	0	0	1100
			6	50	66	6	21	30	68	0	6	0	6	179	50			29.83	1400	0	2000	0	0	1000
			6	50	66	6	21	30	70	0	6	0	4	179	50			29.83	2000	0	3500	0	0	4000
	Alice	F	6	60	66	9	16	15	87	3	6	0	9	172	7.5	0	3	28.67	0	300	100	0	0	200
			6	60	66	9	16	15	90	1	2	0	3	172	7.5			28.67	200	0	600	0	0	200
			6	60	66	9	16	15	72	0	0	0	0	172	7.5			28.67	100	300	700	0	0	0
			6	60	66	9	16	15	113	0	0	0	0	172	7.5			28.67	0	100	100	0	0	0
	Thyrea	F	9	35	53	11	25	30	58	1	4	0	5	163	14.5	0.33	7.5	27.17	0	0	1000	200	0	400
			9	35	53	11	25	30	94	1	6	0	7	163	14.5			27.17	0	300	0	0	0	500
			9	35	53	11	25	30	50	3	10	1	13	163	14.5			27.17	0	300	1300	0	0	1300
			9	35	53	11	25	30	688	0	5	0	5	163	14.5			27.17	0	100	500	0	0	500
	Charissa	F	7	30	50	8	25	25	63	0	0	0	0	145	13	0	0.25	24.17	0	100	1000	0	0	0
			7	30	50	8	25	25	57	0	1	0	1	145	13			24.17	0	500	1400	0	0	0
			7	30	50	8	25	25	119	0	0	0	0	145	13			24.17	0	100	2900	0	0	500
			7	30	50	8	25	25	111	0	0	0	0	145	13			24.17	0	0	3000	0	0	400
	Cassandra	F	10	60	60	10	23	40	106	0	1	0	1	203	1.6	0	0.4	33.83	0	0	1000	0	0	0
			10	60	60	10	23	40	101	0	0	0	0	203	1.6			33.83	0	0	100	0	0	0
			10	60	60	10	23	40	99	0	0	0	0	203	1.6			33.83	0	200	0	0	0	0
			10	60	60	10	23	40	8	0	0	0	0	203	1.6			33.83	0	0	300	0	0	0
			10	60	60	10	23	40	7	1	0	0	1	203	1.6			33.83	0	0	100	0	0	0
	Lycus	M	6	50	65	10	25	30	46	0	3	0	3	186	9.33	0	2	31	0	0	1400	0	0	600
			6	50	65	10	25	30	20	0	2	0	2	186	9.33			31	200	100	100	0	0	300
			6	50	65	10	25	30	105	0	1	0	1	186	9.33			31	200	0	200	0	0	400
	Valgius	M	16	26	56	19	23	25	47	1	0	0	1	165	19.17	0.17	1.67	27.5	200	0	1300	200	0	600
			16	26	56	19	23	25	15	2	0	0	2	165	19.17			27.5	600	300	400	400	0	700
			16	26	56	19	23	25	43	1	0	0	1	165	19.17			27.5	600	0	1700	300	100	1600
			16	26	56	19	23	25	19	3	0	0	3	165	19.17			27.5	200	0	700	400	0	200
			16	26	56	19	23	25	11	1	0	0	1	165	19.17			27.5	0	200	400	0	600	400
			16	26	56	19	23	25	31	1	2	1	3	165	19.17			27.5	0	500	900	3500	0	600

Appendix 3.1 (cont): Reflectance measurements and parasite loads

Lemur species	Name	Sex	crown	cheek	chest	back	out.leg	rump	Sample no.	*Strong.f1*	*Strong.f3*	*Lemuricola*	*Strongyloides*	Tot. bright.	Av. load	Av *Lemur.*	Av. *Strong.*	Mean Br.	*e* (eggs/g)	*h*	*asc*	*k*	*d*	*s*
Lemur catta	Philocles	M	4	35	55	8	22	20	95	0	3	0	3	144	9.86	0	3.71	24	400	0	400	0	0	0
			4	35	55	8	22	20	102	1	10	0	11	144	9.86			24	700	500	0	0	0	0
			4	35	55	8	22	20	92	0	4	0	4	144	9.86			24	400	0	0	0	0	200
			4	35	55	8	22	20	13	0	2	0	2	144	9.86			24	500	400	0	0	0	400
			4	35	55	8	22	20	55	0	2	0	2	144	9.86			24	700	0	0	0	0	0
			4	35	55	8	22	20	1	0	1	0	1	144	9.86			24	700	0	100	0	0	300
			4	35	55	8	22	20	115	0	3	0	3	144	9.86			24	400	0	600	0	0	100
	Cercops	M	11	43	64	16	22	31	52	0	5	0	5	187	15	0	3.5	31.17	300	0	300	0	0	800
			11	43	64	16	22	31	114	0	2	0	2	187	15			31.17	800	700	0	0	0	1100
	Charops	M	8	44	63	11	16	22	44	1	0	0	1	164	12.2	0	2.2	27.33	0	100	200	0	0	1000
			8	44	63	11	16	22	98	0	0	0	0	164	12.2			27.33	100	0	100	0	0	100
			8	44	63	11	16	22	71	0	0	0	0	164	12.2			27.33	1100	0	400	0	0	0
			8	44	63	11	16	22	2	0	10	0	10	164	12.2			27.33	300	200	400	0	0	100
			8	44	63	11	16	22	14	0	0	0	0	164	12.2			27.33	700	800	1000	0	0	0
	Aracus	M	7	80	56	9	22	34	45	0	3	0	3	208	8.83			34.67	200	0	300	0	0	100
			7	80	56	9	22	34	17	1	1	0	2	208	8.83			34.67	100	0	0	0	0	200
			7	80	56	9	22	34	118	4	7	0	11	208	8.83			34.67	100	0	100	0	0	300
			7	80	56	9	22	34	112	0	2	0	2	208	8.83			34.67	300	0	500	0	0	0
			7	80	56	9	22	34	5	1	1	0	2	208	8.83			34.67	0	0	0	0	0	0
	Agnostes	M	9	76	62	15	21	27	97	2	4	0	6	210	20.67	0	4.67	35	300	0	500	200	0	1600
			9	76	62	15	21	27	4	0	4	0	4	210	20.67			35	400	0	2400	0	0	2200
			9	76	62	15	21	27	110	1	3	0	4	210	20.67			35	0	100	1100	0	0	300

Appendix 3.1 (cont): Reflectance measurements and parasite loads

Species and Group	Sex	Sample	Count1	Count 2	Count 3	Count 4	*Ascaris lumbricoides* worms
Madagascar:							
Lemur catta							
Tan East	M	493	2t 1f	2 t 2f	1 t	1 f	0
Tan East	M	485	0	1 t	3 t	0	0
Red	M	433	1 t	0	0	0	0
Red	M	453	5 t	1 t	4 t	3 t	0
Red	M	413	0	0	0	0	0
Red	F	420	0	1 t	0	0	0
Red	F	400	3 t	0	6 t	3 t	1
Green	F	93	1 t	0	0	0	0
Green	F	459	16 t	8 t 2 f	10 t 2 f	15 t 3 f	1
Yellow	M	439	0	0	0	0	0
Yellow	M	495	0	0	1 t	0	0
Yellow	F	445	0	0	0	0	0
Lavender	F	492	1 t	1 t 2 f	1 t	0	0
London zoo:							
Varecia varecia	F	1	0	0	0	0	0
Eulemur macaco	M	2	0	0	0	0	0

Appendix 3.2: Parasite counts for wild and captive lemurs

NB: t = *Ascaris lumbricoides* oocytes
f = *Ascaris lumbricoides* oocytes (unfertilised)

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Addendum

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